Structure and dynamics of lowland podocarp-broadleaved forest in the Central North Island, New Zealand

The effects of different silvicultural regimes on stand structure and tree species composition

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This thesis is dedicated to my parents,
who inspired and always supported
my scientific ventures.

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Abstract

Podocarp-broadleaved forests and their alliances form one of the largest forest groups in New Zealand and cover an area of approximately 2.9 million hectares. Their vast exploitation and deterioration in the past 150 years called for sustainable forest management as an imperative need. As a consequence, commercial harvesting of these forests is restricted to private land only and is strictly controlled by the Ministry of Primary Industries under the Forests Act 1949 as amended in 1993. The Act demands sustainable management of podocarp-broadleaved forest in a form of selective harvesting of podocarps that is limited to single trees or small groups. But there is concern that selective harvesting of podocarps in this forest type is not sustainable due to the complex structure of those forests.

This thesis explores the regeneration dynamics in an old-growth podocarp-broadleaved forest in the Central North Island and how past harvesting has altered its structure. Tree core analysis is an important tool to obtain information on tree age and growth. As *Beilschmiedia tawa* is the dominant tree species in this forest and as little is known about the suitability of tree cores of this species in age and increment studies, their prospects and limitations are elaborated first. The second study examines the structure of old-growth podocarp-broadleaved forests and the natural processes that drive recruitment success and failure. In the third study, the impact of different sizes of harvesting gaps on tree species regeneration and subsequent growth is investigated. The final chapter evaluates harvesting prescriptions in the Forests Act on the basis of key findings of the above studies.

The results demonstrate that false and missing rings are common features in *B. tawa* tree cores but that individual errors in the form of overestimation and underestimation of calculated increments cancel each other out on a stand basis, making stand level predictions reliable. They further illustrate that the scarcity of large-scale disturbances in old-growth podocarp-broadleaved forest is responsible for a regeneration gap of the podocarps *Dacrydium cupressinum*, *Dacrycarpus dacrydioides*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia* and *Podocarpus totara* but that harvesting can improve their growth conditions significantly if the gaps created are large enough. This is, however, not in accordance with the low-impact harvesting prescriptions in the Forests Act, while the results presented here show that selective harvesting of emergent podocarps is not sustainable and accelerates the decline of those species in this forest type.

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Chapter 1

Introduction

1.1. The past

The native forests of New Zealand played an important role in the development of the country's early economy. It was not least for the forests and quick profits that the first Europeans came to these islands in the late 18th century, as the timber found here was of exceptional quality (J. Halkett & Sale, 1986). From that time on, the natural wealth of the North Island was ruthlessly exploited and no thought was given to the future of the forests (Governor-in-Chief of New Zealand, 1851; Sale, 1978). From the beginning of the nineteenth century, timber was exported in vast quantities to Australia, Europe and the USA for a poor financial return (Ministry of Works, 1964; Reed, 1953a). Even though timber soon became a foundation of New Zealand's economic prosperity, short-sighted policy misused vast amounts of highly valuable timber for railway sleepers, fencing posts, mining props, butter boxes, and numerous other purposes (Reed, 1953b). In addition, forest was often seen as 'wasteland' and vast areas were cleared and turned into 'valuable' farmland (Reed, 1953a).

By the early 20th century, the government realised that natural forests were not going to meet New Zealand's long-term timber needs. A transition in the timber industry had to take place to meet the needs of a growing nation, and the export of New Zealand timber became restricted by the Commissioner of State Forests, Sir Francis Bell and the Board of Trade in 1918 (F. H. Bell, 1919). Nonetheless, Lands Department predicted that *Agathis australis* and *Dacrycarpus dacrydioides* supplies (the most valuable native tree species at that time) would be exhausted in some years' time (House of Representatives, 1918). Less valuable species such as *Dacrydium cupressinum* became in some places the mainstay of the industry. In 1918, a forests department with the responsibility for forestry management was established to avoid a future shortage of timber supplies. However, it was not before this department was transformed into the State Forest Service that sustainable forest resource management was attempted (Ellis, 1920).

D.E. Hutchins, a British forester with great expertise who had moved to New Zealand in 1915, recommended large-scale re-establishment of indigenous forests to assure a permanent timber supply (Hutchins, 1919), a view shared by L. MacIntosh Ellis, the first Director of Forests (Ellis, 1920; House of Representatives, 1921). But after appraising the

results of the national forest inventory in 1923 and calculations of the annual level of timber consumption, Ellis turned to exotic afforestation with *Pinus radiata* and *Pseudotsuga menziesii*. He was convinced that the demand for forest products could not be provided by the indigenous forest resource base for much longer than the mid-1960s. In addition, he instigated research studies on regeneration and growth rates of indigenous tree species on a contract basis to Auckland and Canterbury University Colleges. The botanist Leonard Cockayne, who was involved in this research, consequently recommended sustained-yield forestry with beech in his work on New Zealand beech forests (Cockayne, 1926, 1928a).

In these early days, planting trials with exotic tree species were linked with indigenous forestry and large plantations were established during the first planting boom of exotic trees during the Depression of the 1920/30s to ensure that New Zealand remained self-sufficient in timber after the expected exhaustion of native timber in the mid-1960s. On the other hand, enthusiasts like Rudolph Hohneck, who came to New Zealand in 1899 without any formal forestry education, developed management systems for indigenous forests similar to modern Continuous Cover Forestry (Barton, 2008) following Hutchins' 1919 report (Barton, 2007). By 1954, the output of exotic sawn timber exceeded the production of indigenous species. But new timber use predictions (Ward, 1956) pointed again to shortfalls by the year 2000. As a consequence, a second planting boom of exotic forests began in the mid 1960s.

Early botanical and ecological investigations revealed difficulties in indigenous forestry such as long maturing periods of podocarps (House of Representatives, 1946). In addition, species like *D. dacrydioides*, *Prumnopitys taxifolia* and *Podocarpus totara* were found to prefer soils which were best for dairy farming (House of Representatives, 1947). Despite a few selective harvesting trials that were established in the early 1960s, the Forest Service failed to implement sustainable systems of silviculture of indigenous forests, and plantations with native trees apparently performed poorly. The environmental awakening in the 1970s and 1980s led to a change in indigenous forest policy which now promoted sustainability through selective harvesting. But the demand for native wood was still very high and selective harvesting often resembled clearfelling (M. Roche, 1990).

With the election of a Labour government in 1984, major administrative changes took place, leading to the disestablishment of the New Zealand Forest Service in 1987 and the creation of a Department of Conservation (DOC), a Ministry of Forestry and a Forestry Corporation. This put an end to most harvesting of native forests on public land, giving the responsibility for National Parks, Scenic and other Reserves and indigenous State Forests with no timber extraction to DOC. In 1990, Timberlands West Coast Ltd. was established to manage remaining state indigenous production forests following the West Coast Accord from 1986, including 9,500 ha of *D. cupressinum* forest and 45,000 ha of beech forest (Hilliard, 1998).

In 1993, the Forests Act 1949 was amended by the Government to end unsustainable forestry (M. Clarke, 1992). In particular, Amendment Part 3A covers the legislation that is governing indigenous forestry on private land and includes harvesting, milling and trading timber. It does, however, not apply to planted indigenous forest. But the obstacles for private landowners to harvest and mill under the new legislation were high and the whole market collapsed, leaving behind native forests without economic value to their owners (Heath, 1993). While the Ministry of Forestry promoted sustainable forest management of indigenous forests on private land, the West Coast Accord was cancelled in 2000 and beech forests were removed from proposed Timberlands West Coast's management. By 2002, the government ceased all indigenous production forestry on publicly-owned land, even though these forests were almost the only ones with a history of sustainable management (Heath, 1992).

1.2. The present

The present Forests Act gives private landowners four options of harvesting indigenous forest and milling native timber. To be able to trade native timber from indigenous forests, landowners have to provide either a sustainable forest management (SFM) plan (50-year term) or a sustainable forest management permit (10-year term). For personal use, they have to apply for a milling certificate which enables them to harvest and mill up to 50 m^3 native timber. In addition, milling certificates can be issued for the use of salvage wood and trees that are removed for the construction and maintenance of access routes. All sawmills processing native timber have to be registered (Ministry of Agriculture and Forestry, 2009).

Planted indigenous forest on land that was not under indigenous forest immediately before planting is exempt from these regulations.

Currently, around 89,068 ha of privately owned indigenous forest are managed in New Zealand for timber production under 53 registered SFM plans and 139 SFM permits (Ministry for Primary Industries, 2016). This corresponds to a permitted annual harvest of around 89,391 m³ standing volume (Table 1).

Table 1. Approved Sustainable Forest Management (SFM) Plans and Permits in New Zealand (Ministry for Primary Industries, 24. November 2016), forest area (ha) and permitted annual harvesting volume ($m^3\ yr^{-1}$) per species

Species	**SFM Plans**		**SFM Permits**		**Total**
Gymnosperms	**($m^3\ yr^{-1}$)**	**(ha)**	**($m^3\ yr^{-1}$)**	**(ha)**	**(m^3)**
Agathis australis	-	-	42.4	221	42.4
Dacrycarpus dacrydioides	164.6	26,428	12.6	613	177.2
Dacrydium cupressinum	2,972.9	54,352	1,185.0	25,842	4,157.9
Phyllocladus trichomanoides	175.0	6,131	5.7	171	180.7
Podocarpus cunninghamii	40.2	3,306	1.3	58	41.5
Podocarpus totara	146.2	24,688	183.0	1,856	329.2
Prumnopitys ferruginea	555.0	49,860	41.2	2,797	596.2
Prumnopitys taxifolia	112.3	29,013	65.0	4,474	177.3
Angiosperms					
Beilschmiedia tarairi	-	-	14.2	230	14.2
Beilschmiedia tawa	6,034.3	37,060	717.6	13,051	6,751.9
Dysoxylum spectabile	-	-	0.2	11	0.2
Elaeocarpus dentatus	232.8	33,059	1.1	46	233.9
Elaeocarpus hookerianus	31.0	15,754	-	-	31.0
Fuscospora cliffortioides	2,654.4	15,863	1.8	80	2,656.2
Fuscospora fusca	31,236.4	39,322	462.0	1,902	31,698.4
Fuscospora solandri	1,344.0	3,775	71.2	621	1,415.2
Fuscospora truncata	1,105.8	2,966	446.4	58	1,552.2
Knightia excelsa	357.9	18,187	53.5	2,682	411.4
Kunzea ericoides s.l.	5.0	836	-	-	5.0
Laurelia nova-zelandiae	47.0	2,329	-	-	47.0
Leptospermum scoparium	5.0	836	-	-	5.0
Litsea calicaris	1.0	8,132	-	-	1.0
Lophozonia menziesii	35,936.6	51,349	427.0	2,301	36,363.6
Metrosideros robusta	147.0	16,861	-	-	147.0
Metrosideros umbellata	563.0	12,277	-	-	563.0
Nestegis cunninghamii	5.0	8,132	0.6	128	5.6
Quintinia sp.	12.1	1,093	-	-	12.1
Vitex lucens	-	-	3.3	205	3.3
Weinmannia racemosa	1770.4	14,831	-	-	1770.4
Weinmannia silvicola	-	-	0.7	70	0.7
Total	**85,654.9**	**60,858**	**3,735.7**	**28,209**	**89,390.6**

Out of the total number of 192 license holders, 47 % of the area and 63 % of the annual harvest are managed under only 4 licences, accounting for 80 % of the annual harvest of *Lophozonia menziesii* and 54 % of *Fuscospora fusca*.

A total of 1.2 million hectares of indigenous forest are privately owned, of which 400,000 ha could be sustainably managed for timber production in the future (Ministry for Primary Industries, 2017a). The potential for indigenous forestry in New Zealand is highlighted by the increasing demand for high-quality specialty timbers, which cannot be fulfilled by current exotic plantations that are heavily dominated by *Pinus radiata*. The revenue stream that incorporates the mill entry price of timber, milling labour and the end user price is estimated to potentially generate $114 million annually if harvesting levels were at the allowed maximum of current plans and permits. If all privately owned native forests that are suitable for forestry would be managed under SFM plans or permits, the annual revenue could even reach $462 million (KPMG, 2013).

The annual import of sawn angiosperm and gymnosperm timber is presumed to have more than doubled from 34,000 m³ in 2010 to over 72,000 m³ in 2016, with value increasing from $46.4 million to over $92.3 million. In addition, imports of veneer are presumed to have increased from 2,544 m³ in 2010 to over 12,450 m³ in 2016. Even the import of wooden furniture is presumed to have increased even from $189 million in 2010 to over $357 million in 2016.[1]

Some countries from which sawn timber, sleepers and furniture are imported are known to use illegal and unsustainable harvesting (Dauvergne & Lister, 2011; Katsigris et al., 2004; Turner, Buongiorno, Katz, S. Zhu, & R. Li, 2008). But the 'Customs and Excise (Sustainable Forestry) Amendment Bill 48-1' which was trying to stop New Zealand's import of timber and wood products produced illegally or unsustainably was defeated by the New Zealand Parliament on 18. November 2009. The protection of native trees in New Zealand at the expense of timber taken from sources that are detrimental to biodiversity in other countries reflects a self-interested attitude within New Zealand (Salmon, 2003). To provide specialty

[1] 2016 data are provisonal (Ministry for Primary Industries, 2017b)

woods without depleting biodiversity overseas and to enhance biodiversity in native forests in New Zealand are still major challenges of indigenous forestry.

Sustainable forestry ventures in New Zealand, based upon diverse forest ecosystems dominated by indigenous tree species, offer a potential win-win opportunity for providing a sustainable supply of high-value wood products with all its social and economic benefits (Devoe & Olson, 2001; Fairweather, Blackburn, Swaffield, & Hock, 2003; Gillman, 2008; Norton, 2003) as well as being beneficial in restoring habitat to support native biodiversity (Norton, 1996), carbon sequestration, and soil and water protection.

1.3. The problem

It is of crucial importance to understand the ecological processes in New Zealand's indigenous forests, as only silviculture that is based on a comprehensive knowledge of forest dynamics provides the basis for sustainable forest management following the requirements of the current Forests Act. In addition, the more complex and diverse a forest ecosystem is, the more important is the comprehension of its dynamics.

For many years, Manaaki Whenua-Landcare Research New Zealand has undertaken intensive research on sustainable indigenous forestry and its effects on forest ecosystems, and the research presented in this thesis builds on achievements attained by this research institute.

Lophozonia menziesii and *F. fusca* are the two species that are currently the main focus of indigenous forestry (Table 1). They often grow in relatively species-poor forest alliances that are mainly dominated by one or two beech species (Wiser, Hurst, E. F. Wright, & Allen, 2011), and harvesting ranges from selective logging to coupes up to 0.5 ha with varying success (Allen, Hurst, & Wiser, 2012). But the largest percentage of New Zealand's indigenous forests originally comprised mixed forests with varying abundances of gymnosperm and angiosperm species. These forests are complex ecosystems with multiple canopy species of varying dominance and age (Allen, Bellingham, Holdaway, & Wiser, 2014). Today podocarp-broadleaved forests and all their alliances cover an area of approximately 2.9 million hectares (Wiser et al., 2011).

Podocarp species of the genera *Dacrycarpus*, *Prumnopitys*, *Dacrydium* and *Podocarpus* are among the most valuable tree species in New Zealand. Their vast exploitation and deterioration in the past 150 years show the imperative need for sustainable forest management which cannot be achieved without understanding their growth dynamics. Using natural resources requires responsible environmental thinking, where the balance of natural regenerative processes has to be maintained (Baumgart, 1979).

While the call for sustainable management of native forests is strong, the criteria for and indicators of sustainability often remain unclear (Wijewardana, 1996). Knowledge of indigenous forests and the impact of harvesting was in the past considered inadequate by several authors, and sustainable management is sometimes used as a slogan rather than as an achievable approach for forestry (Field, 1995). In beech forest, science is trying to close this knowledge gap by monitoring harvesting operations and providing management systems (Allen et al., 2012) that are based on ecological research (Hurst, 2014).

Originally, sustainability was a pure economic term that equated to yield sustainability, the harvest of an annual volume that does not exceed the average growth rate of the forest (Carlowitz, 1713). But the current definition of sustainable forest management in New Zealand includes ecological, cultural and other non-economic outputs as well and is defined in the Forests Amendment Act 1993 (New Zealand Government, 2009) as:

"... the management of an area of indigenous forest land in a way that maintains the ability of the forest growing on that land to continue to provide a full range of products and amenities in perpetuity while retaining the forest's values"

Maintaining biological diversity, enhancing soil and water protection as well as carbon storage are important criteria for present-day forest management (Allen, Bellingham, & Wiser, 2003). Only when all these criteria are taken into account, a forest can be managed sustainably. A change from research on individual species to ecosystem research is one of the major preconditions for sustainable management (Allen & Benecke, 1997). In particular, the impact of commercial timber extraction from indigenous forests needs comprehensive

research. It is important to develop silvicultural systems that minimise the environmental impacts of harvesting (Allen & Benecke, 1997). A silvicultural system that follows natural dynamics of forests has to be based on extensive knowledge in forest ecology (James & Norton, 2002). Causes and impacts of canopy disturbance, regeneration, and relative abundance and growth of individual species are key factors of forest dynamics. These vary from site to site and from forest to forest, and an adaptive approach of silviculture is necessary in order to meet the requirements of sustainable forest management (Allen, Norton, Benecke, & Wiser, 2002; Benecke, 1996).

According to Schedule 2.10 of the Forests Act 1949 (Provisions relating to sustainable forest management plans, inserted as from 1 July 1993 by section 6 Forests Amendment Act 1993 No. 7), the sustainable forest management prescriptions demand that:

> ***"... the rate of harvest from a forest ... shall be limited to a level at which the forest can continue to supply an annual or periodic non-diminishing yield in perpetuity ..."*.**

Management prescriptions in the Forests Act differentiate between podocarp and kauri (*Agathis australis*) forest, beech forest and shade-tolerant exposure-sensitive broadleaved species. While beech forest "***shall be harvested only in coupes of 0.5 hectares or less***", podocarps and kauri forest as well as shade-tolerant exposure-sensitive broadleaved forest "***shall be harvested only by single tree or small group harvesting using low impact techniques***" (New Zealand Government, 2009).

In podocarp and kauri forest, "***harvesting shall, as far as possible, be restricted to the selective removal of trees predisposed to windthrow or early death***" while "***the character and structure of all parts of the forest shall be maintained***" (New Zealand Government, 2009).

In shade-tolerant exposure-sensitive broadleaved forest, the law further prescribes that "***regard shall be had for natural regeneration characteristics of the species targeted for logging***" (New Zealand Government, 2009).

Where podocarps, kauri or shade-tolerant species are harvested and "***sufficient advanced growth is lacking, there shall be planted for each tree removed at least 5 nursery-raised seedlings of at least 60 centimetres in height of the same species***" (New Zealand Government, 2009). The seed of those seedlings should be collected from the district, where they are to be planted.

When regeneration in beech forest fails, "***the failure shall be corrected by the planting of nursery-raised seedlings ...***" (New Zealand Government, 2009).

The harvesting prescriptions for podocarps essentially resemble early selective harvesting that was carried out in the early 1960s (Beveridge & Herbert, 1978). Single tree and small group harvesting were supposed to mimic natural small-scale disturbances as they occur after windthrow, where the extraction of one or more trees forms gaps of different sizes (Benecke, 1996). These methods are regarded as the practices of choice for sustainable forestry of mixed old-growth podocarp-broadleaved. In addition, planting of seedlings was supposed to compensate a possible lack of natural regeneration.

Research investigating the long term effects of selective harvesting suggested that the size of harvested gaps might be an important factor for successful regeneration and advanced growth of the different tree species in mixed podocarp-broadleaved forest (M. C. Smale, Fitzgerald, Arnold, & Bartlam, 2008). The current legislation seems to ignore the fact that these ecosystems are extremely complex with numerous tree species inhabiting different light environments (Carswell, Richardson, Doherty, Allen, & Wiser, 2007). Selective harvesting of those ecosystems might favour some species at the expense of others (Berry, Phillips, Ong, & Hamer, 2008). In particular, light-demanding tree species might not be able to benefit from small canopy gaps (Ebbett & Ogden, 1998). For successful sustainable forest management, it is therefore important to understand the natural potential of the different tree species to adapt to a light regime that is manipulated by harvesting.

The overall objective of this doctoral research is to investigate whether the current harvesting prescriptions meet the intent of the current Forests Act in New Zealand for

sustainable forest management or if they alter the structure of the forest in an undesirable way.

This thesis is divided into 4 chapters that focus on different elements of forest dynamics research and regeneration ecology:

Study 1 **The nature of growth**

A standard method for dendro-ecological research as well as age and increment studies of trees is tree ring analysis. The accuracy of the results depends on the fulfilment of certain underlying assumptions. Their violation can cause substantial error in estimates. Tree ring analysis was used for age estimation of trees and the analysis of their past radial increment. While work on this subject has been done for several native gymnosperm tree species, little is known about the reliability of tree cores for age and increment studies of *Beilschmiedia tawa*, a dominant tree species in podocarp-broadleaved forest in the central North Island. This study investigates the performance and suitability of *B. tawa* tree cores in age and increment studies.

Study 2 **Podocarp-broadleaved forest in the Central North Island**

A prerequisite for sustainable forest management is the recognition of natural processes that determine a forest structure. In particular, stand history and successional pathways are important for understanding the current structure of a forest. This study examines the history of podocarp-broadleaved forest in the central North Island, the current forest structure at the study site and its future, as well as natural factors that influence this development.

Study 3 **The positive impact of large disturbance**

Selective harvesting aims to mimic small-scale natural disturbances in order to minimise the adverse effects of tree removal while maintaining the natural composition and structure of a forest. But not every tree species favours those small disturbances, and light-demanding species might prefer different scales of disturbances than shade-tolerant species. In this study, the effect of different-sized harvesting canopy gaps on tree species regeneration and subsequent growth are investigated 56 years after high-grading and 52 years after selective harvesting. It elaborates requirements of the different tree species involved for regeneration and subsequent growth, and illustrates the impact of low disturbance single-tree or small group harvesting on the forest structure.

Conclusion **Sustainable management of podocarp-broadleaved forest**

Based on findings of the different studies, silvicultural prescriptions specified in the current Forests Act will be assessed for podocarp-broadleaved forest. This chapter will examine whether forest management that follows those prescriptions is sustainable in the context of the Forests Act and meets its objectives.

The final question will be:

Can selective harvesting of
old-growth podocarp-broadleaved forest
be sustainable at all?

1.4. The challenge of forest classification – what is a podocarp-broadleaved forest?

This doctoral research is focusing on podocarp-broadleaved forest in New Zealand. But what defines a podocarp-broadleaved forest? Is it a single forest type? How can it be distinguished from other forest types? A review of past and current definitions highlights the challenges in classifying these forests.

Forests are constantly changing and adapting ecosystems, with their structure and composition altering over time (Allen & Norton, 2000). In addition, the indigenous forests in New Zealand comprise of hundreds of different species of plants and animals and due to their complexity, a classification of these forests is a challenging task. Early botanists had little idea of ecology, and only a few reliable descriptions on New Zealand's forest species and communities are found in scientific literature of the time (Kirk, 1899). By the early 20th century, wide areas of New Zealand were still botanically unexplored or imperfectly known, and it was not until 1913 that different botanical districts were described in a more-or-less comprehensive manner based on 'typical examples' (Cockayne, 1928b). This classification system followed with some modifications earlier German work on plant-geography using floristic and ecological characteristics (Warming & Vahl, 1909). But no attempt at completeness was made due to the great variety of plant communities in New Zealand and the inaccessibility of so many of them. It was not until the mid-1950s that ecologists in the North Island used structural differences and the presence and relative abundance of physiognomically prominent trees on a larger scale to classify forests. Even though the composition of about 30% of the forests was reasonably well known, understanding of forests in remote areas and hill country was still fragmentary. Based on aerial photographs and data collected during the extensive National Forest Survey of 1946-1955 (Masters, Holloway, & McKelvey, 1957; Thomson, 1946), North Island native forests were classified into 78 forest types in 18 groups (McKelvey & Nicholls, 1957) (Table 2).

Table 2. North Island forest group (McKelvey & J. L. Nicholls, 1957)

Forest groups	
Agathis group (Type A1 – A4)	Characterized by densely stocked upper tier of *Agathis australis*
Beilschmiedia tawa – *Agathis* – podocarp group (Type B1 – B5)	Generally a multi-tier structure with *Agathis australis* being emergent or concentrated on ridges; mosaic of virgin forest and forest exploited for *Agathis*
Nothofagus – *Agathis* group (Type C1 – C2)	Characterized by dense *Nothofagus spec.* and scattered *Agathis australis*
Metrosideros – *Dacrydium* – *Beilschmiedia tawa* group (Type D1 – D8)	Scattered emergent *Metrosideros robusta* and *Dacrydium cupressinum* with a dense tier of *Beilschmiedia tawa* underneath
Metrosideros – *Dacrydium* – *Beilschmiedia tarairi* group (Type E1 – E3)	A northern variant of the D group
Metrosideros – *Dacrydium* – *Weinmannia* group (Type F1 – F2)	Scattered emergent *Metrosideros robusta* and *Dacrydium cupressinum* with a dense tier of *Weinmannia racemosa* underneath
Podocarpus cunninghamii – *Weinmannia* group (Type G1 – G4)	Scattered and sometimes emergent *Podocarpus cunninghamii* with a dense tier of *Weinmannia racemosa* underneath
Nothofagus – podocarp – *Beilschmiedia tawa* group (Type H1 – H5)	Upper tier of dense *Nothofagus spec.* with scattered podocarps and *Beilschmiedia tawa* in lower tiers
Nothofagus – *Dacrydium* group (Type I1 – I4)	Dense upper tier of *Nothofagus* sp. with scattered *Dacrydium cupressinum*
Nothofagus – *Podocarpus cunninghamii* group (Type J1 – J2)	Dense upper tier of *Nothofagus* sp. over scattered *Podocarpus cunninghamii*
Nothofagus group (Type K1 – K9)	Dense upper tier of pure *Nothofagus* sp.
Podocarp group (Type L1 – L4)	Characterized by dense upper tier of podocarps; represents colonisation following forest destruction
Prumnopitys taxifolia – *Dacrydium cupressinum* group (Type M1 – M8)	Scattered emergent podocarps over dense angiosperm tier; represents a later stage of forest succession than group L
Beilschmiedia group (Type N1 – N6)	Mainly types that have been exploited for podocarps, leaving stands of *Beilschmiedia* sp.
Nothofagus – *Beilschmiedia* group (Type O1 – O2)	Former Type H forest that has been exploited for podocarps
Weinmannia group (Type P1 – P3)	Human-induced angiosperm forest, dominated by *Weinmannia racemosa*
Coastal forest group (Type Q1 – Q3)	Coastal forest
Scrub group (Type R1 – R4)	Scrub forest as a first stage of colonisation

This was the first time that a complete picture of the indigenous forest pattern of the North Island was drawn. This classification was later revised and many hitherto poorly known forest types were added (J. L. Nicholls, 1976), and the classification was extended later to the South Island (McKelvey, 1984). Forest types were now grouped into classes, determined only by the specific association of trees with a dbh (diameter in breast height, 1.4 m above ground) >30 cm in high forest (canopy height >15 m) and 10-30 cm in short forest (J. L. Nicholls, 1976). Based on some 48 tall and medium-sized tree species, and over 70 smaller tree species normally not exceeding 10 m in height and the variation in their ecological tolerances and community relationships, these forest types were later grouped into 4 major indigenous forest types: conifer-broadleaved forests of the lower altitudes, high-altitude conifer-broadleaved forests, coastal forests and beech forests (P. Wardle, 1991).

When exploitation of indigenous forests evolved into management in 1975 as a result of the revised Indigenous Forest Policy (New Zealand Forest Service, 1977), another more management-oriented approach to the classification of indigenous forests was developed (Beveridge, 1979). For management purposes, podocarp forests were described as forests that contain major podocarp tree species such as *D. cupressinum*, *D. dacrydioides*, *P. taxifolia*, *Prumnopitys ferruginea* and *P. totara* in varying abundances (Beveridge, 1983; McKelvey, 1984). Depending on the content of merchantable trees, podocarp forests were now divided into five management categories (Table 3).

Table 3. Management categories of podocarp forests in New Zealand (Beveridge, 1983)

Management category	**Merchantable podocarp trees per ha**	**Merchantable volume of podocarp trees per ha**
Dense podocarp forest	50-90	300-600 m^3
Medium-density podocarp forest	20-50	100-300 m^3
Low-density podocarp forest	< 20	< 100 m^3
Logged podocarp forest	Removed	Removed
Second-growth podocarp forest	Varying	Varying

In 1981, the National Water and Soil Conservation Organization began a classification project using vegetative cover groups of dominant plant formations such as Grassland, Scrub and Forest as well as their binary groups Grassland-Scrub, Grassland-Forest and Forest-Scrub (Newsome, 1987). In total, three levels and eight vegetative cover groups and 47 vegetative cover classes were classified, based on 6,000 vegetation entities in the New Zealand Land Resource Inventory (Table 4). This approach made large-scale mapping of New Zealand's vegetation cover possible for the first time, with the smallest unit covering about 800 ha.

Table 4. Vegetative cover classes in New Zealand based on 6,000 vegetation entities in the New Zealand Land Resource Inventory (Newsome, 1987)

Vegetative cover groups	**Vegetative cover classes**	**Area (ha)**
Cropland	C1 – Orchards or vineyards and pasture	97,000
	C2 – Horticultural crops and pasture	67,000
Grassland	G1 – Improved pasture	6,447,000
	G2 – Unimproved pasture	891,000
	G3 – Short tussock grassland	1,114,000
	G4 – Snow tussock grassland	1,361,000
	G5 – Short tussock – snow tussock grassland	715,000
	G6 – Red tussock grassland	76,000
Grassland-Scrub	GS1 – Grassland and mixed indigenous scrub	856,000
	GS2 – Grassland and *Leptospermum* scrub or fern	2,284,000
	GS3 – Grassland and *Cassinia* scrub	39,000
	GS4 – Tussock grassland and sub-alpine scrub	966,000
	GS5 – Grassland and *Dracophyllum* scrub	49,000
	GS6 – Grassland and gorse scrub	234,000
	GS7 – Grassland and matagouri	510,000
	GS8 – Grassland with sweet brier or sweet brier and matagouri	232,000
Scrub	S1 – Mixed indigenous scrub	362,000
	S2 – *Leptospermum* scrub or fern	626,000
	S3 – Sub-alpine scrub	96,000
	S4 – Gorse scrub	20,000
Grassland-Forest	GF1 – Pasture and podocarp-broadleaved forest	340,000
	GF2 – Pasture and broadleaved forest	133,000
	GF3 – Pasture and beech or podocarp forest	129,000
	GF4 – Pasture and exotic forest	19,000
	GF5 – Tussock grassland and beech forest	101,000
	GF6 – Tussock grassland and podocarp-broadleaved forest	10,000

Vegetative cover groups	Vegetative cover classes	Area (ha)
Forest-Scrub	FS1 – Kauri and Leptospermum or mixed indigenous scrub	47,000
	FS2 – Podocarp-broadleaved forest and scrub	446,000
	FS3 – Podocarp-broadleaved-beech forest and scrub	139,000
	FS4 – Beech forest and scrub	314,000
	FS5 – Beech-broadleaved forest and scrub	48,000
	FS6 – Broadleaved forest and scrub	177,000
	FS7 – Sub-alpine scrub and indigenous forest	88,000
	FS8 – Exotic forest and scrub	18,000
Forest	F1 – Podocarp forest	43,000
	F2 – Lowland podocarp-broadleaved forest	1,091,000
	F3 – Highland podocarp-broadleaved forest	51,000
	F4 – Lowland podocarp-broadleaved-beech forest	1,399,000
	F5 – Highland podocarp-broadleaved-beech forest	205,000
	F6 – beech forest	1,992,000
	F7 – Beech-broadleaved forest	114,000
	F8 – Broadleaved forest	223,000
	F9 – Exotic forest	1,212,000
Miscellaneous	M1 – Sub-alpine or alpine herb field	187,000
	M2 – Wetland communities	89,000
	M3 – Sand-dune communities	52,000
	M4 – Pakihi heathland communities	45,000

Recently, the need for a more detailed classification with greater partitioning led to a new approach following the International Vegetation Classification (IVC) by designating classified units as 'alliances' based on 1177 spatially representative plots on a 8 x 8 km grid (Wiser et al., 2011). Here, 24 alliances comprising 19 to 105 plots each were recognized and forest alliances were designated into four physiognomic-based forest groups: *Nothofagus* forest (five alliances), *Nothofagus*-broadleaved forests (four alliances), Nothofagus-broadleaved-podocarp forests (four alliances) and Broadleaved-podocarp forests (four alliances) (Table 5). Still, the grid size of 8 x 8 km makes it very difficult to cover rare forest types and further refinement is under way. This is the first published quantitative classification of New Zealand's woody vegetation based on an objective plot layout (Wiser et al., 2011).

Table 5. Forest groups and alliances in New Zealand following the international vegetation classification based on 1177 spatially representative plots (IVC) (Wiser et al., 2011); *Nothofagus* species were renamed into *Fuscospora* and *Lophozonia*

Forest group	Alliance	Area (ha)
Nothofagus forest	*Hoheria glabrata – Coprosma pseudocuneata – Olearia ilicifolia* (*Lophozonia menziesii*)/*Polystichum vestitum* low forest and subalpine shrubland [alliance 7]	189,000
	Fuscospora solandri (*Peraxilla tetrapetala*)/(*Coprosma pseudocuneata*) subalpine forest [alliance 8]	151,000
	Fuscospora solandri – Lophozonia menziesii / *Coprosma pseudocuneata – Hymenophyllum multifidum* forest [alliance 9]	492,000
	Lophozonia menziesii – Fuscospora fusca – Fuscospora solandri forest [alliance 10]	144,000
	Fuscospora solandri – (*Fuscospora fusca*) / *Coprosma microcarpa – Leucopogon fasciculatus* forest [alliance 11]	166,000
Nothofagus-broadleaved forests	*Weinmannia racemosa – Griselinia littoralis – Pseudowintera colorata* / *Blechnum discolor* forest [alliance 12]	612,000
	Carpodetus serratus – Pseudowintera colorata – Aristotelia serrata (*Lophozonia menziesii*) / *Blechnum discolor* forest and successional shrubland [alliance 13]	189,000
	Lophozonia menziesii – Griselinia littoralis – Myrsine divaricata / *Coprosma foetidissima* forest [alliance 14]	484,000
	Lophozonia menziesii – Weinmannia racemosa – Fuscospora fusca / *Blechnum discolor* forest [alliance 15]	711,000
Nothofagus–broadleaved-podocarp forests	*Weinmannia racemosa – Metrosideros umbellata – Fuscospora solandri* / *Coprosma foetidissima* forest or tall shrubland [alliance 16]	371,000
	Pseudowintera colorata – Griselinia littoralis – Fuscospora fusca (*Lophozonia menziesii*) / *Microlaena avenacea* forest [alliance 17]	454,000
	Weinmannia racemosa – Cyathea smithii – Prumnopitys ferruginea / *Blechnum discolor* forest [alliance 18]	371,000
	Weinmannia racemosa – Cyathea dealbata – Knightia excelsa (*Beilschmiedia tawa*) / *Leucopogon fasciculatus* forest [alliance 19]	348,000
Broadleaved-podocarp forest	*Weinmannia racemosa – Prumnopitys ferruginea – Dacrydium cupressinum* / *Blechnum discolor* forest [alliance 20]	794,000
	Melicytus ramiflorus – Cyathea smithii – Dicksonia squarrosa – Carpodetus serratus (*Beilschmiedia tawa*) forest [alliance 21]	393,000
	Beilschmiedia tawa – Weinmannia racemosa – Melicytus ramiflorus / *Ripogonum scandens* forest [alliance 22]	522,000
	Cyathea dealbata – Melicytus ramiflorus – Freycinetia baueriana – Ripogonum scandens forest [alliance 23]	605,000
	total:	6,996,000

According to the latest classification, the various broadleaved-podocarp forest groups and alliances cover an area of around 3,858,000 ha, representing one of the largest forest groups in New Zealand. The majority of these forests are found in lowland regions and it has been proposed that they reflect an unstable pattern (Robbins, 1962) where the composition and structure of many of these forests have continuously changed through geological time (Fleming, 1977; McGlone, 1997). Research on climatic changes and geomorphologic processes shows that these forests were always adapting and readjusting to a dynamic environment undergoing frequent changes (Baumgart, 1979; McGlone, 1983a; McGlone & Moar, 1977; Ogden, Fordham, Horrocks, Pilkington, & Serra, 2005).

In the context of this thesis, the term podocarp-broadleaved forest described by Newsome (1987) will be used to emphasize the forest component this study focuses on – the podocarps and their relationship to the broadleaved species within that forest type, even though this term is interchangeable with the term broadleaved-podocarp forest (Wiser et al., 2011) which emphasizes the dominance of angiosperms within the forest. Other terms that are frequently used in literature for this forest type are conifer-angiosperm forest (Lusk, Jorgensen, & Bellingham, 2015; M. C. Smale et al., 2016), conifer-broadleaved forest (M. C. Smale & P. N. Smale, 2003; M. C. Smale, Richardson, & Hurst, 2014), podocarp-tawa forest (M. C. Smale & Kimberley, 1986; M. C. Smale, Beveridge, Pardy, & Steward, 1987; M. C. Smale, Fitzgerald, & Bartlam, 2008) or conifer-hardwood forest (M. C. Smale & Beveridge, 2007).

1.5. Research area

Most of the once widespread forests in New Zealand were destroyed by humans (Ewers et al., 2006). Since the beginning of Maori settlement, almost 40 % of New Zealand's native forests have been lost to human-induced fires before 1840 (McGlone, 1983b; McWethy, Whitlock, Wilmshurst, McGlone, & X. Li, 2009; Perry, Wilmshurst, McGlone, & Napier, 2012; Perry, Wilmshurst, McGlone, McWethy, & Whitlock, 2012). With the arrival of Europeans, forest destruction reached an industrial scale with large areas being cleared for farmland, exotic plantations or to accommodate for housing (Fleet, 1986). Overall, the indigenous

forest cover was reduced from 81.1 % in pre-human times to 23.4 % at present, representing a loss of 71.1 % of indigenous forests (Leathwick et al., 2002, 2003). The lowland forests were particularly affected by human destruction (G. R. Stevens, McGlone, & McCulloch, 1995).

With relatively few accessible podocarp-broadleaved forests left unlogged, the selection of suitable research areas that enable a side by side comparison of old-growth forest and harvested forest presented a challenge. To investigate the long-term effects of different silvicultural regimes, study sites had to be harvested decades ago without any subsequent management. The only site that met those requirements was found c. 10 km north of Pureora village in the northern part of Pureora Forest Park in the central North Island on undulating plateau at an elevation of 550-570 m a.s.l. (Figure 1).

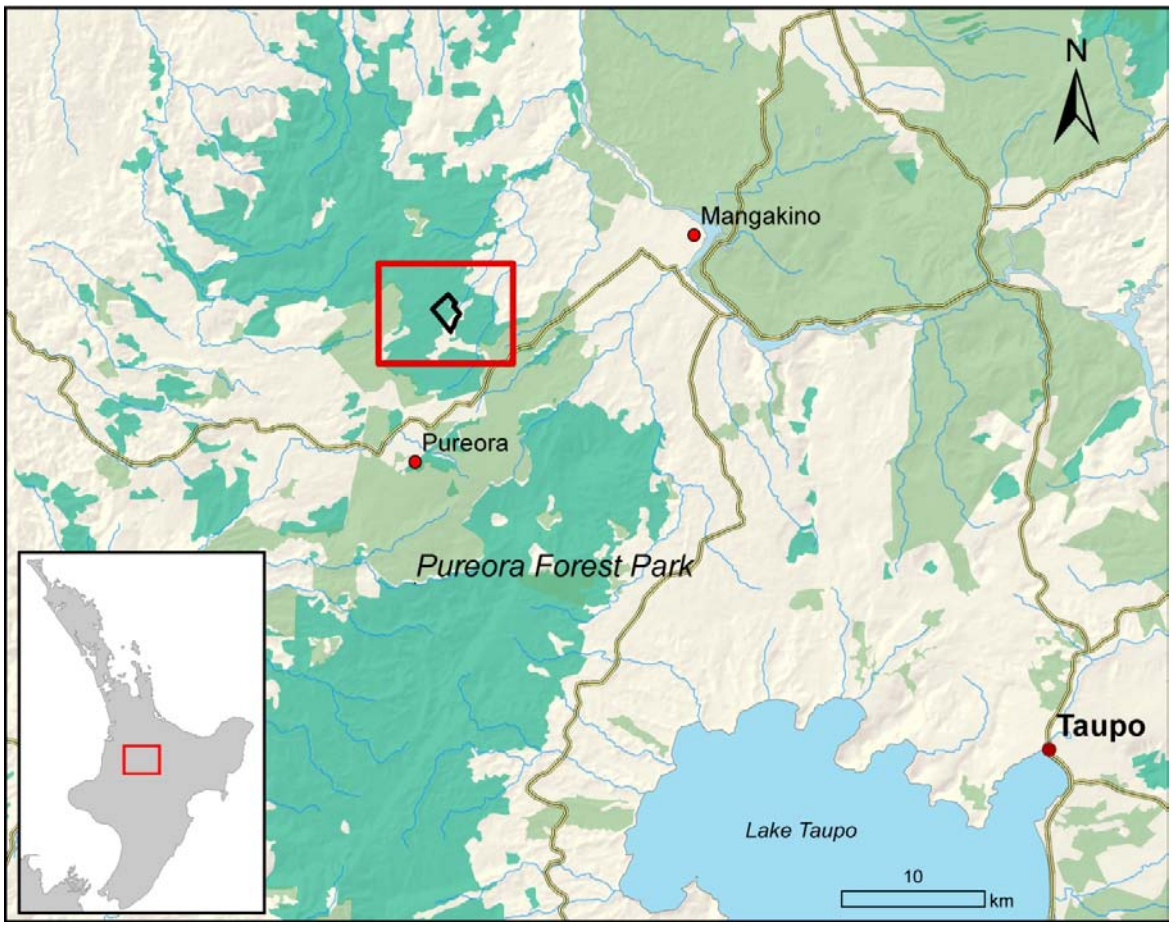

Figure 1. Study site in the northern part of Pureora Forest Park on the Volcanic Plateau in the central North Island

With a size of 17,500 ha, the northern part of Pureora Forest Park includes the Mangatutu and Waipapa Ecological Areas. Even though intensive harvesting affected over 6,000 ha of this forest between 1945 and 1978 (Gaukrodger, N. A. Ritchie, & C. M. King, 2015), large tracts of mostly undisturbed mixed podocarp-broadleaved forest still remain (Figure 2).

Figure 2. Old-growth podocarp-broadleaved forest in the northern part of Pureora Forest Park with 50 m tall podocarps

The plateau was formed by ignimbrite flows from Taupo lava between 750,000 and 300,000 years ago and is covered by rhyolitic tephra (Healy, 1982; J. L. Nicholls, 1986). The tephra themselves are covered by podzolised Pumice soils of various depths that originate from the Taupo eruption of c. A.D. 232 (Hewitt, 1998; Rijkse, 1981). In particular, soils of the Tihoi Series (strongly podzolised Pumice soil) and the Owawenga series (composite of Pumice on Allophanic soils) occur in mosaic form. Soil acidity of mesic soils rises with increasing depth from pH 3.8 (F-Horizon) and pH 4.2 (E-Horizon) to ph 5.5 (B-Horizon) for the Tihoi series, and from pH 3.7 (F-Horizon) and pH 4.1 (E-Horizon) to ph 4.9 (B-Horizon) for the Owawenga

series, attributed to strong leaching (C. J. West, 1986). Levels of phosphorus as well as of magnesium, potassium and calcium are low in these strongly leached soils (Rijkse, 1981, 1984).

The climate on the Volcanic Plateau is cool-temperate (Holdridge, 1967) and slightly continental with warm summers and cool winters. The plateau is not directly affected by mountain ranges and prevailing winds are generally light (Hessell, 1986). However, destructive storms occur from time to time and can cause severe forest damage (e.g., 1915, 1936, 1958). The meteorological station at Pureora (NZMS station C8551, altitude 549 m) recorded average annual temperatures of 10.3°C (16°C in summer, 6°C in winter) with day maxima of 30°C and minima of -9°C in the period 1941-70. The average rainfall in the same period was averaged at 1830 mm in 180 rain days. Ground frost can be expected on 87 days yr^{-1} while snow is a rather rare phenomenon, occurring on average only on 2 days yr^{-1} (Lowe & C. M. King, 2015).

1.6. Harvesting

The study site comprises extensive old-growth podocarp-broadleaved forest, two blocks of Maori freehold land (Table 6) that were high-graded in 1956/58 and adjacent forest, where a selective harvesting trial was carried out in 1961 by the Forest Research Institute (FRI) within what is now the Waipapa Ecological Area (Leathwick, 1987) (Figure 3). With the help of aerial photographs and data collected during the first National Forest Survey from 1947 to 1957 (Masters et al., 1957), the old-growth forest and the harvested areas were classified as medium density podocarp-broadleaved forest (M2) with emergent *P. taxifolia* and *D. cupressinum* over a dense canopy of *B. tawa* (McKelvey & J. L. Nicholls, 1957). Other frequent species in this forest type are *P. ferruginea*, *Elaeocarpus dentatus* and *Weinmannia racemosa* as well as locally prominent *D. dacrydioides* and *P. totara*.

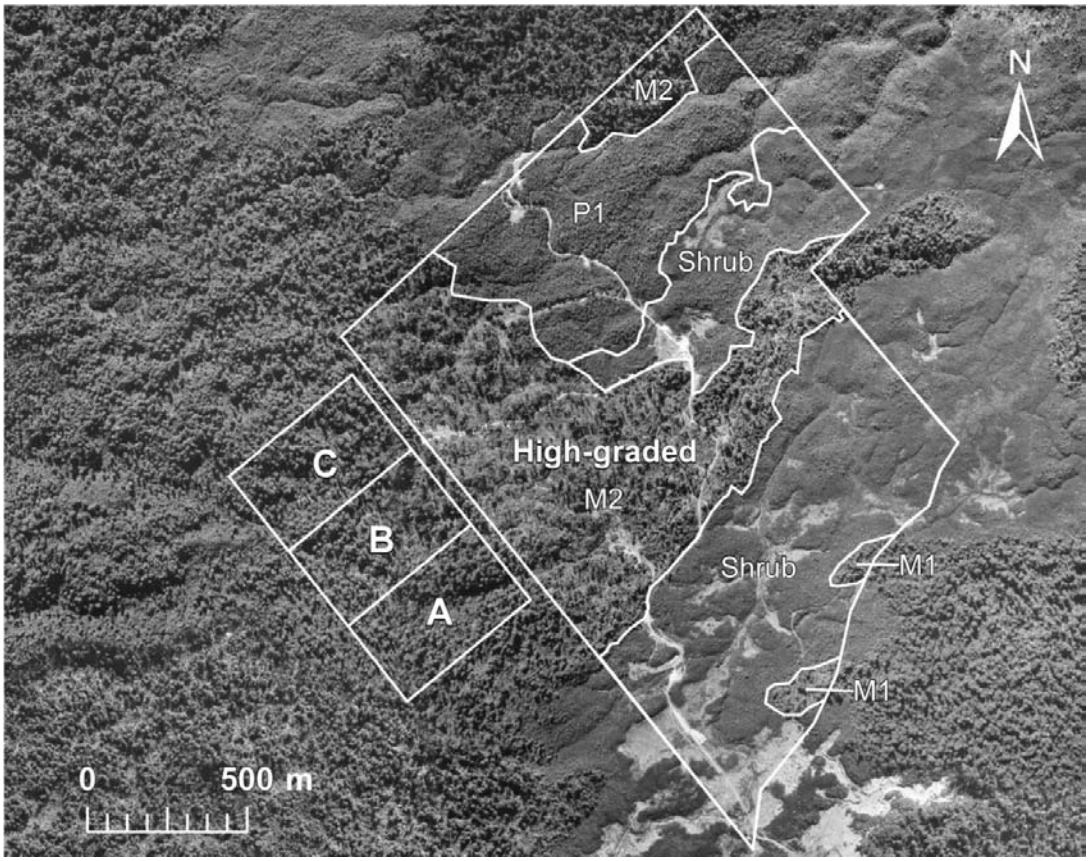

Figure 3. Study site in the Pouakani Block of Purora Forest Park. A, B and C show the different blocks of the 1961 selective harvesting trial, while the area adjacent to the East demarcate a 100 ha block of Maori freehold land that was high-graded between 1956 and 1958. (Ortho Photography: NZ Aerial Mapping, 1963; vegetation types P1, M1, M2 and Shrubs are based on McKelvey & Nicholls (1957) and Leathwick (1987) (Table 2))

A large part of the Maori land is covered by fire-induced secondary forest of *W. racemosa* and *Knightia excelsa* (P1) (McKelvey, 1963; McKelvey & J. L. Nicholls, 1957) and frost flats (plateau with depressions where frosts can occur year-round) dominated by *Dracophyllum subulatum* and *Gaultheria spp.* shrubs (Leathwick, 1987).

Table 6. Size and ownership of the Maori Freehold Land that was high-graded in 1956/58

Block	ID	Size	Shares	Owners
Wharepuhunga-Pouakani	4005	95.4337 ha	6.2	165
Wharepuhunga-Pouakani-Maraeroa	4006	148.7806 ha	154.444	144

1.7. Species in focus

The tree species found at the study site belong to various orders and families of gymnosperms and angiosperms. As the main canopy species are mainly restricted to the gymnosperm families Podocarpaceae and the angiosperm families Lauraceae and

Elaeocarpaceae, this study focuses primarily on the 8 species in Table 7. The details of size and life span provided for each species are only averages and individual values can differ widely. This is also the case for the site requirements stated for each species. Some podocarp species such as *D. cupressinum* and *P. ferruginea* can tolerate quite extensive shade when they are young (Lusk et al., 2015). But the light requirements of species can change between different life stages, where they need higher light conditions for advanced growth (Lusk, Duncan, & Bellingham, 2009).

At earlier life stages of these species, competition with other tree species and in particular tree fern species can be quite severe. Under certain circumstances this competition can even prohibit regeneration (Beveridge, 1973; Coomes et al., 2005). Therefore, all species occurring at the study site are included in the frequency and abundance studies as soon as they reach 1.4 m height.

Table 7. Main canopy species in focus of this study; species characteristics provided by Enright & Ogden (1995), Dawson (2011), Wardle (2011), Knowles & Beveridge (1982) and Allen et al. (2002)

scientific name	common name	size	life span	site requirements
Gymnosperms:				
Dacrycarpus dacrydioides	kahikatea	up to 65 m tall; dbh up to 2.5 m	c. 600 years	Favours moist, free-draining and fertile sites; light-demanding
Dacrydium cupressinum	rimu	up to 60 m tall; dbh up to 2 m	c. 650 years	Favours well-drained and reasonably fertile sites; tolerant of poorly drained soils; fairly shade-resistant
Phyllocladus trichomanoides	tanekaha	up to 25 m tall; dbh up to 1 m	c. 300-500 years	Mainly found on well-drained, dry soils; light-demanding
Podocarpus totara	tōtara	20- 30 m tall; dbh up to 2 m	c. 900 years	Favours well-drained fertile soils; intolerant of wet soils; light-demanding
Prumnopitys ferruginea	miro	Up to 25 m tall; dbh up to 1 m	c. 650 years	Similar to *D. cupressinum*, shade-tolerant
Prumnopitys taxifolia	matai	20-30 m tall; dbh up to 1.3 m	c. 600 years	Favours fertile well-drained soils; light-demanding
Angiosperms:				
Beilschmiedia tawa	tawa	Up to 25 m tall; dbh up to 1 m	c. 400 years	Favours moderately fertile soils; very shade-tolerant
Elaeocarpus dentatus	hinau	15-20 m tall; dbh up to 1 m	c. 300 years	Favours fertile, moist soils, light-demanding

Chapter 2

The nature of growth – *Beilschmiedia tawa* tree ring analysis and its limitations in age and increment studies

2.1. Introduction

2.1.1. Ring formation

For more than a century, tree ring analysis has been an important tool in age and growth increment studies in New Zealand (W. R. B. Oliver, 1931). Based on the work of Douglass (1935) and Zeuner (1946), tree ring analysis became in the middle of the 20th century also an important tool for dendrochronology in New Zealand (Batley, 1956; V. Bell & R. E. Bell, 1958; Golson, 1955; Lockerbie, 1950). In the following 40 years 65 chronologies of several Podocarpaceae, Araucariaceae, Cupressaceae and Nothofagaceae species were developed (Ahmed & Ogden, 1985; Dunwiddie, 1979; LaMarche, Holmes, Dunwiddie, & Drew, 1979; Norton, 1983a, 1983b, 1989; Norton & Ogden, 1987; Palmer, Ogden, & Patel, 1988). More and more species become the focus of tree ring analyses. In increment studies as well as in studies that use tree-ring sequences to age trees (e.g., for studies of stand history), there are two problems associated with tree ring analysis: the annual formation of rings and the representativeness of the ring widths.

2.1.2. Annual ring formation

Many tree species in New Zealand form a distinct xylem boundary with the appearance of a ring when their cambial activity ceases between growing seasons (Bussell, 1968). But this annual formation of rings has been questioned from early on (J. Stewart, 1905). It was assumed that several gymnosperm species such as *Agathis australis* and *Dacrydium cupressinum* might form more than one ring per year (Hutchinson, 1926). This was confirmed by Sando (1936) who found 46 complete rings in an *A. australis* that was only 34 years old. Lloyd (1963) also found this to be quite common, with *D. cupressinum* producing as many as three complete rings per year. He observed a similar pattern for *A. australis* and other native gymnosperms such as *Podocarpus totara* and *Dacrycarpus dacrydioides* resulting in age estimation errors of up to 65 %. These `false` rings in fast growing trees were often found to be discontinuous, not extending around the whole circumference of the tree (D. A. Franklin, 1969). In slow growing trees, these `false` rings can be very difficult to separate from `true` rings and the accurate counting of tree rings can be impossible. Where

seasons are more distinct, such as in subalpine regions, problems around the annual ring formation seem to be less marked. Wardle (1963) observed annual ring formation in 22 subalpine shrub and tree species and found that *Phyllocladus* and *Libocedrus* were among the most promising genera for dendrochronological studies, forming distinctive and clearly visible rings. Similar observations were made by Norton (1984), who found distinct annual rings in subalpine *Lophozonia menziesii* and *Fuscospora cliffortioides*.

2.1.3. Environmental factors influencing ring width

Tree growth is affected by several external factors such as water, temperature, light, carbon dioxide, oxygen and soil minerals (Fritts, 1976). Many of these environmental conditions change throughout the long life-span of a tree. Some of them may change frequently whereas others may only change after many years. They all either enhance or limit tree growth. Favourable conditions for tree growth result generally in wider tree rings than in situations where conditions are unfavourable. Trees that are growing in the understorey of a forest show generally narrower rings than dominant canopy trees of the same species. Changes in these conditions can affect a few trees only (e.g., localized wind-throw) or a whole forest (e.g., warm and dry summer). In general, it can be expected that trees which experience the same conditions show similar growth patterns where wide and narrow tree rings alternate in certain intervals. The influence of an individual factor is the larger, the more this factor is limited. This is the case for example with water on dry sites or in arid areas and temperatures in boreal forests (Schweingruber, 1993).

2.1.4. Representative ring width in tree cores

Distinct growth patterns occur in particular where climatic factors have a strong influence on tree-ring variability. This is the case where tree species grow at their distributional limit (Cook & Kairiukstis, 1990). Those distinct patterns are used in dendrochronology to identify false or missing rings through cross-dating (Norton & Ogden, 1987). But where tree growth is less influenced by distinct seasons or changes in limiting growth factors, such as in New Zealand lowland forests, cross-dating of species such as *D. cupressinum* and *D. dacrydioides*

was found to be challenging, where even ring patterns of trees from the same area might not match (Cameron, 1960).

Tree growth studies rely on representative measurements of basal increment. Therefore long term studies use repeated dbh measurements to quantify individual tree growth. But where this information is not available, tree growth is often deducted from measurements of tree ring widths along a single radius. This implies that the width between two rings in a given year is representative for a tree's growth in that particular year, which might not always be the case (Norton, Palmer, & Ogden, 1987).

2.1.5. Species-specific ring formation

From early on, irregular annual growth was observed in many native New Zealand species, where trees did not grow evenly around their circumference. Instead, tree ring widths were found to vary by up to a factor of 5 at different points around the circumference (J. Stewart, 1905). This can be due to `wedging out` of rings when trees show an eccentric growth form where the chronological centre does not match the geometrical centre of a tree. But even well-formed trunks are known to show `wedging` in a lobate form (Hutchinson, 1926; Norton et al., 1987). Species where this growth form was observed include the gymnosperms *D. cupressinum*, *P. totara*, *D. dacrydioides*, *Prumnopitys taxifolia* and *Prumnopitys ferruginea* (Figure 4). But angiosperms such as *Beilschmiedia tawa* were also found to show wedging and lobate growth (Dunwiddie, 1979). Hutchinson (1926) and Franklin (1969) also add `fluting` (conspicuous vertical ridges and grooves) as an extreme but common form of irregular growth at the base of larger *D. cupressinum*. Here, the ring width was found to vary even by a factor of 12. Trees were found to show this type of growth from around 100-200 years and it appeared most prominent when trees are 400-700 years old (Hutchinson, 1926).

Figure 4. Irregular annual growth with wedging and lobate rings in a 76 year old *Prumnopitys ferruginea*.

2.1.6. Tree species in focus of tree ring research

Most studies of tree rings in New Zealand have focused on gymnosperm tree species because of their economic importance (D. A. Franklin, 1966; G. H. Stewart & J. C. White, 1995). The only angiosperms that underwent closer investigation were the New Zealand`s beeches, which were regarded as highly valuable timber species (Cockayne, 1921, 1928a). These species showed similar patterns in ring formation to the ones found in gymnosperms. Nevertheless, Bussell (1968) found that *L. menziesii*, *Fuscospora fusca* and *Fuscospora cliffortioides* can produce two flushes of growth per year, forming two rings with the second additional ring being incomplete.

In the mid 1950s, foresters searched for native species that could replace the fast diminishing resource of gymnosperm trees. One potential species was *B. tawa*, but the

annual nature of its ring formation was in doubt. McKelvey (1954) claimed that the visible parenchymatous bands do not necessarily reflect annual rings and that growth analyses of *B. tawa* should not be carried out using tree rings. In addition, Dunwiddie (1979) described ring wedging and lobate growth in *B. tawa*. But in another study (Ogden & C. J. West, 1981), cross sections of eight *B. tawa* were examined and a clear correlation between tree rings and annual growth found, leading them to the conclusion that tree rings in *B. tawa* are annual. But these authors confine their results to fast growing trees, as parenchyma bands were found to form in *B. tawa* whenever growth is slowed down by environmental factors.

2.1.7. Tree age estimation based on increment cores

While most authors initially used tree discs for age estimation, non-destructive sampling methods such as tree-coring have become more popular (Cameron, 1957; Dunwiddie, 1978), leading to further problems. Norton, Palmer and Ogden (1987) described problems occurring with *A. australis*, *Libocedrus bidwillii*, *F. cliffortioides* and *P. taxifolia*. Besides the slow growth of native trees in New Zealand that can produce very narrow rings with `wedging out` of rings which can lead to an underestimation of age, there are other problems closely related to tree-coring. In situations where coring fails to reach the chronological centre of trees, the missing rings must be extrapolated. The sampling height is also of importance as the time it takes a tree to reach coring height must be added to the total number of rings counted. Even though the mean error for aging the above species was found to be less than 10 %, it can be as large as 78 % for individual trees (Norton et al., 1987). In addition, the occurrence of `false` rings has to be taken into account. Based on the analysis of 12 discs of *D. dacrydioides*, Duncan (1989) calculated an error of age underestimation of 3 % for missing rings in 48 theoretical cores and 35 % for the failure of 84 theoretical cores to reach the chronological centre. He proposed that sampling along the longest radius of a tree can reduce this error.

2.1.8. Growth studies based on increment cores

Repeated measurements of diameters are the most common method to estimate diameter growth of trees. The disadvantages of diameter measurements are that (a) no information is

available for tree growth occurring before the first measurement was carried out and (b) measurements have to be repeated after substantial diameter growth occurred (J. S. Clark et al., 2007). Even though in theory, this could be annual for very fast growing species (*Eucalyptus* spp.*)*, in most cases economic reasons dictate a longer period. In the case of slower growing native trees in New Zealand, periods between diameter measurements can be as long 20 years (M. C. Smale, Fitzgerald, & Bartlam, 2008). Another problem with repeated diameter measurements in slow growing trees is that they have to be made in exactly the same place and way. Differences in measured height as well as loose bark or moss can lead to significant errors. But long intervals pose the problem that no information is available on annual growth. Instead, annual growth is interpolated on the basis of periodic increment (Biondi, 1999).

Another method of diameter growth estimation is based on dendrometer bands (Hall, 1944; Liming, 1957). Even though these can be read annually, no information is available for growth that occurred before the bands were installed. In addition, the time and costs involved for installation, reading and maintenance reduce their application to permanent sampling plots.

Therefore, increment cores have become an important tool for growth studies, where annual as well as historical growth is important or economic drivers prohibit repeated diameter measurements. Even though growth studies based on increment cores are time consuming, they are not necessarily confined to small studies and were used in large surveys as well. For example, Hornbeck et al. (1988) used increment cores of 5000 trees of 10 species during a forest health study in New England.

2.1.9. Underlying assumptions of growth studies based on increment cores

The use of increment cores for growth studies was developed in the Northern Hemisphere for tree species growing in climates with distinct annual growing seasons and that show a regular circumferential growth. The underlying assumptions for those studies can be summarized as: (1) trees do have symmetrical growth, which means that if a tree is growing in one year twice as much as in the following year, the tree ring will be over the whole

circumference of the tree twice as wide as the one of the following year; (2) there is no `wedging` with tree rings fading out; (3) the tree does not exhibit lobate growth and shows no fluting; (4) the tree core represents the actual annual growth rates of the tree; (5) there are no undetectable `false` or `missing` rings and the number of rings in the core being the same along all radii.

In native tree species in New Zealand, these underlying assumptions are often found to be violated and results of growth studies can carry uncertainties that make their reliability questionable (Hutchinson, 1926), especially when it is not possible to cross-date the ring patterns.

2.1.10. *Beilschmiedia tawa* in the focus of increment studies

Beilschmiedia tawa is an evergreen angiosperm tree species endemic to New Zealand. It is often the most dominant canopy tree species in old-growth lowland podocarp-broadleaved forest in the North Island and the northeast of the South Island (Allen et al., 2014; Newsome, 1987; Wiser et al., 2011). Due to its silvicultural potential (Hinds & Reid, 1957; McKelvey, 1954; M. C. Smale & Beveridge, 1987; M. C. Smale, Bathgate, & Guest, 1986), it has been for some years the focus of several ecological studies (M. C. Smale et al., 2014; C. J. West, 1986, 1995) where tree core analysis is an important tool. Yet it is still questionable to what degree tree cores can be used for ageing and to calculate the annual increment of *B. tawa* trees.

The wood of *B. tawa* is diffuse-porous, with slightly distinct to distinct growth rings and vessels that are to a greater extent evenly distributed throughout the ring (Meylan & Butterfield, 1978). These vessels are mainly solitary but can also occur in clusters. Axial parenchyma cells form bands that are up to 13 cells wide and clearly visible (Knowles & Beveridge, 1982). Uniseriate and multiseriate rays that are up to 7 rays wide indicate the direction to the pith. More detailed information on the wood anatomy of *B. tawa* including illustrations and electron micrographs can be found in Meylan & Butterfield (1978) as well as Knowles & Beveridge (1982).

2.1.11. Focus of this study

This study focuses on the applicability and reliability of *B. tawa* tree cores for age and increment studies. The following main questions were investigated:

1. **Can tree cores of *Beilschmiedia tawa* be used for tree age estimation?**

2. **Can tree cores of *Beilschmiedia tawa* be used to calculate annual diameter increments?**

A set of detailed questions was posed around those main questions to account for the reliability and uncertainties of tree core estimates.

What is the relationship between bark thickness and tree diameter?

How reliable are calculated historic diameters of trees based on tree cores?

How large is the difference between calculated and measured periodic increments?

How do estimates based on different tree cores of the same tree compare?

Do cores of trees of all social classes lead to similar results?

How variable are ring widths within tree cores?

How can ring width patterns be used to account for false and missing rings?

What is the effect of false and missing rings in tree cores on age and increment studies?

What is the relationship between missing / false rings and annual increment?

To answer these questions, repeated historical diameter measurements of trees in mixed podocarp-broadleaved forest in the Central North Island of New Zealand are compared with diameters computed on the basis of increment cores (CP-study). In a second study, numbers of rings and annual increments between cores of the same tree taken at the same height are compared (Twin core study). A recommendation on use and limitations of *B. tawa* tree cores for age and increment studies concludes this study.

2.2. Methods

Between 1960 and 1961, a set of 16 permanent circular plots (CP) of 0.04 ha sizes was established by A.E. Beveridge of the Forest Research Institute (FRI) during the selective logging trial (Beveridge & Herbert, 1978) in the Pouakani Block of Pureora Forest Park, Central North Island, New Zealand to investigate the behaviour of *B. tawa* and podocarp regeneration in selectively logged medium-density (McKelvey, 1963; McKelvey & J. L. Nicholls, 1957) podocarp-broadleaved forest (M. C. Smale & Kimberley, 1986). In these plots, all trees with diameters larger than 2 inches (5.08 cm) at 4.5 feet height (1.37 m) were tagged and measured in 1960/61. In 1963, 1964, 1965, 1974, 1976, 1983, 1984 (M. C. Smale & Kimberley, 1986) and 2005 (M. C. Smale & Beveridge, 2007) most of these trees were remeasured (since 2005 in 1.4 m height and measurements in cm) and if necessary retagged. This study was conducted using *Beilschmiedia tawa* trees from the above circular plots and from the surrounding old-growth forest.

2.2.1. Tree bark modelling

Tree diameters are generally measured including bark. But there is little possibility of accounting for historic bark thickness values when dealing with increment cores. As this is an important factor when modelling the annual diameters of trees during their whole lifespan, a study was carried out to evaluate the relationship between tree diameters and bark thickness of *B. tawa* and to find out if it is possible to estimate historic values. For this purpose, 371 bark thickness measurements were taken from randomly selected trees of various diameters.

2.2.2. Radial increment and diameter calculation

For a comparison of historic diameter measurements and values calculated on the basis of tree cores, the annual increments and historic diameters of trees were calculated for their whole life-span using the following range of calculation steps.

1. The shortest distance between the outermost ring and the chronological centre was marked on the core and measured. Following this line, the distance between all adjacent growth rings was measured for each core. For a core failing to reach the chronological centre of a tree it was important to always measure the ring width in direction to the pith. In a perfectly concentric situation, this is the rectangular distance between growth rings (Figure 5) and should follow the wood rays exactly.

Figure 5. Measuring the rectangular distance between growth rings

2. Where a tree core failed to reach the chronological centre of the tree, the missing radius was calculated using the geometrical approach described by Duncan (1989) [equation 1].

$$r = \frac{L^2}{8h} + \frac{h}{2} \qquad (1)$$

where (*r*) is the missing distance to the chronological centre, (*L*) is the length of an inner growth ring arc and (*h*) is the visible height of this growth ring arc (Figure 6).

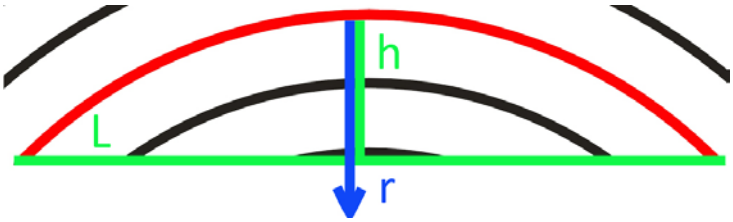

Figure 6. Geometrical calculation of the missing distance to the chronological centre of a tree for cores that failed to reach it

3. To account for any deviation caused by core reading, the radial distance from the outermost ring to the chronological centre was calculated using to the law of cosines [equation 2]. This is the hypotenuse (b) of the right-angled triangle formed by the lengths of the tree core (c) and the missing distance to the chronological centre (a) with the angle β being 90° (Figure 7). This radius should be equal to the sum of

measured ring widths plus the calculated missing distance to the chronological centre (r). If both values were not equal, the individual ring width measurements were not correct and had to be repeated.

$$b = \sqrt{a^2 + c^2 - 2(a * c * \cos(\beta))} \qquad (2)$$

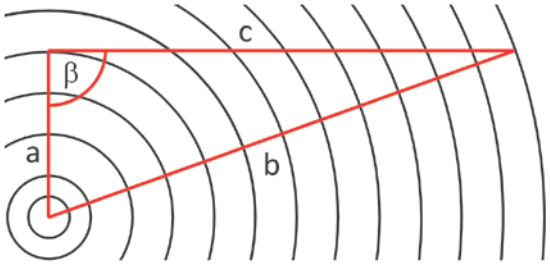

Figure 7. Calculating the tree radius where the increment core was taken

4. The measured tree ring widths were then corrected by the 10° upwards angle at which the core was taken.

5. The number of missing rings was calculated using the length of (r) minus (h) and the mean width of the innermost visible growth rings that share a similar growth. The underlying assumption of this dynamic modelling is that a tree can undergo alternating phases of suppressed and released growth. These phases were observed to be reasonably consistent, with ring widths being autocorrelated, a factor that also has to be taken into account when analyzing the increment data (Speer, 2010). This means that it was assumed unlikely that a tree was suppressed in one year, then released in the next year, suppressed again in the following year and released again in the year after that. The number of rings used to calculate the mean growth of the innermost rings varied between 10 and 40 and were different for each individual increment core.

6. The annual increment of a tree was then calculated taking its eccentricity of growth into account. This was completed with the help of the ratio between the measured increment in each year and the length of the core (distance from the rim to the chronological centre) as well as its measured diameter [equation 3].

$$i_a = \left(\frac{i_m}{l_c}\right) D \qquad (3)$$

where (i_a) is the annual increment in year x, (i_m) is the measured width of the ring in year x based on the tree core, (l_c) is the length of the core (from the rim to the chronological centre) and (D) is the diameter of the tree (measured with a tape).

7. Historic tree diameters were calculated by adding the annual increments of a given number of rings, starting from the latest ring. If the diameter of a tree 50 years ago was to be calculated, the radial increments of the last 50 years were subtracted from the current diameter.

2.2.3. Diameter difference between measured and calculated values – CP study

It was assumed that inter- and intraspecific competition might not only influence the overall growth of a tree but also its ring growth patterns and ring formation processes. Therefore, a total of 86 *B. tawa* were selected from the circular FRI plots in autumn 2014 for a Circular Plot study (CP study) based firstly on their social status (Table 8) which was assumed to reflect their competitive status within the forest ecosystem. Social status is based on biological criteria and was developed by Kraft (1884) as a tree classification system using crown expansion (growth performance) and tree height (dominance) (Pretzsch, 2009). For the New Zealand context, Kraft's system was modified to match the 5-tier-structure of native podocarp-broadleaved forest in the Central North Island. The trees were assigned to 5 different social classes from class 1 to 5 in descending order, where class 3 reflects the lower limit of dominant classes.

Table 8. Number of trees cored in 2014 based on their social class (modified Kraft's (1884) classes)

Social class (status)		2014
1	Predominant (emergents/often older overmature trees)	18
2	Dominant (main canopy trees)	17
3	Codominant (canopy trees with constrained crowns)	19
4	Subdominant (subcanopy trees/regeneration)	18
5	Dominated (understorey trees/regeneration)	14
	Total:	86

Secondly, the trees were selected for their mean annual diameter increment between 1960 and 2014 (Table 9). Even though both characteristics seem to be closely related, as suppressed trees can be expected to be slow growing, subdominant (class 4) and understorey (class 5) trees could be in fact fast growing saplings advancing through the different vertical tiers.

The diameters of these trees were measured in 2014 and the trees cored upwards at an angle of 10° along their longest radii at 1.4 m height. The reason for coring upwards was to prevent water running down along the stem and into the hole (Norton, 1998). The cores were immediately glued onto wooden mounts which minimized shrinkage down to less than 1 %. After air-drying for 3 months, the cores were sanded down with progressively finer grades until the growth rings were clearly visible.

Table 9. Number of samples of trees measured in 2014, based on their mean annual increment

Mean annual increment	Cored trees
< 1.00 mm	22
1.01 - 2.00 mm	25
2.01 - 3.00 mm	28
3.01 - 4.00 mm	11
Total:	86

The diameters were calculated using the method described above and compared with the historic measurements to estimate their congruence (*Diameter difference = Dd*). If no underlying assumptions are violated, the difference between both values should be close to zero. To be able to compare the growth of trees with different diameters in growth studies, radial increments from tree level studies are generally converted into basal area increment as an increment of 1 cm on a 10 cm tree is not equal to a 1 cm increment on a 40 cm tree (Hornbeck et al., 1988). Therefore the above analysis was also carried out for calculated basal areas based on historic measurements and basal areas calculations based on tree cores (*Basal area difference = Bad*).

2.2.4. Effect of social class

It was assumed that dominant trees show different growth behaviour than suppressed trees as they have larger crowns and with that more photosynthesis biomass. They were expected to have larger diameters and larger increment than trees of lower social classes. To test this, the relationship between measured diameters in 2014 and the social status of trees was modelled for all 86 cored trees. Then, the relationship between the mean annual increments of trees for the period 1960-2014 was modelled based on measurements in 1960 and 2014. With those relationships established, the effect of social class on *Dd* was analysed to investigate if different classes share similar values for *Dd*.

2.2.5. Variability of tree rings widths

The widths of consecutive tree rings can be extremely variable (Brienen, Schöngart, & Zuidema, 2016; Schweingruber, 1988; Speer, 2010) and is confirmed for several New Zealand tree species (Dunwiddie, 1979; Norton, Palmer, & Ogden, 1987). These large differences between ring widths can make tree ring dating extremely difficult, if not impossible. But the ability to date rings is an imperative for the detection of false and missing rings and with that for the reliability of increment calculations based on ring widths. For this reason, the variability of tree ring widths was examined and a **mean sensitivity analysis** for 126 tree cores (including the 86 cores from the circular FRI plots plus the 40 additional randomly selected cores from surrounding old-growth forest) was used to investigate the suitability of *B. tawa* tree ring series for ring dating. Here, the year-to-year variability of ring widths was calculated with equation [4].

$$ms_x = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(X_{t+1} - X_t)}{X_{t+1} + X_t} \right| \qquad (4)$$

where *n* is the number of tree rings that are compared, X_t is the ring width in year *t*, and X_{t+1} is the ring width in the year following t (Speer, 2010).

Values for the mean sensitivity analysis range from 0 to 1, where 0 indicates no differences between ring widths. A value close to 1 indicates a maximum difference with every other ring missing. Values around 0.1 were found too complacent and values above 0.4 to sensitive for tree ring dating (Speer, 2010). Values around 0.2 are regarded as optimal.

2.2.6. Differences between two cores of the same tree – Twin core study

Two important underlying assumptions of tree core analysis are that tree rings are formed annually and that the distance between two rings reflects the individual growth of that tree within that year. When these assumptions are fulfilled, analysis of any tree core taken from the same tree and at the same height must lead to the same result of estimations for age and annual increment. To investigate whether or not this is the case for *B. tawa*, 40 large trees (18 trees from circular FRI plots and 22 additional trees from surrounding old-growth forest) with diameters between 30.4 cm and 77.0 cm (mean = 39.5 cm) were randomly selected and were cored twice at the same height, with the second core being taken in a horizontal angle of 90° to the first core. The diameters for every year of a tree's life were calculated for each tree core based on the annual increments. The individual growth pattern of that tree was then used to match these results and to investigate if and to what extent the underlying assumptions were fulfilled or violated. Whether or not one tree core showed false rings or its twin core had rings missing could only be revealed when growth patterns could be related to datable rapid environmental changes.

The example in Figure 8 shows the calculated diameters for two tree cores that differ by 3.5 cm in the year 1957 (yellow arrow). Based on the individual growth pattern of this tree (dashed blue line), this difference can be divided into a horizontal difference (*difference in number of rings = dnr*) of 5 rings and a remaining diameter difference (*actual diameter difference = aDd*) of 1.5 cm. The variable *dnr* is an indicator for false rings / missing rings and the accuracy of age estimates; and *aDd* indicates how representative the tree cores of this tree are for increment studies.

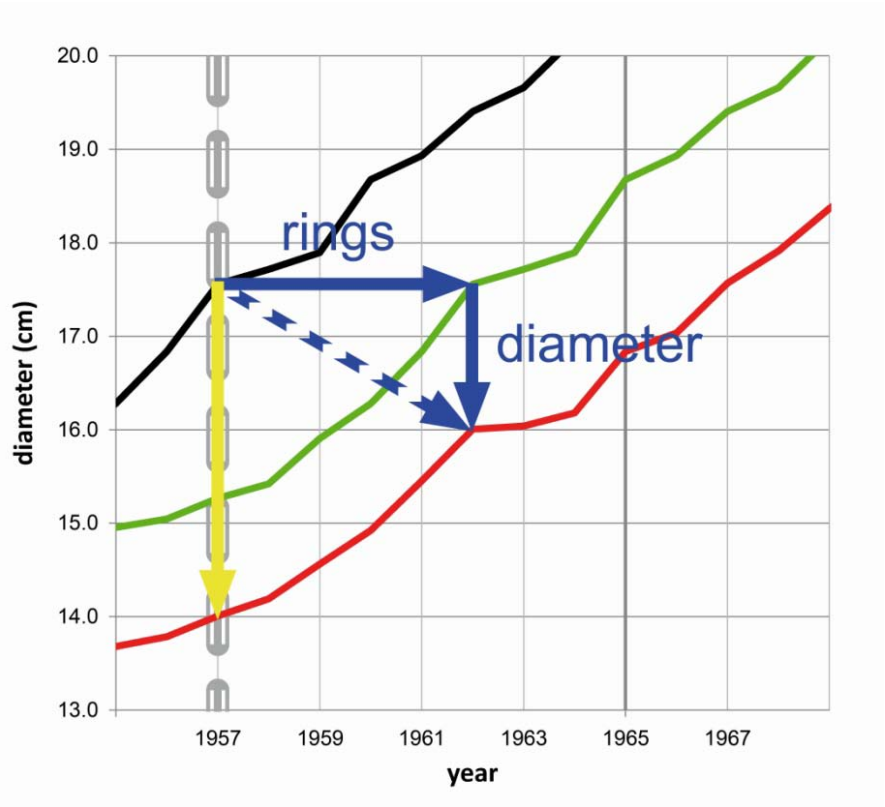

Figure 8. Twin core analysis showing the cumulative growth of a *Beilschmiedia tawa* tree with the black line representing the calculated diameters for core 1 and the red line being core2. The yellow arrow shows the difference between the calculated diameters of both cores (Dd) in the year 1957. The dashed blue arrow indicates the diameter difference in relation to the individual growth pattern. The solid blue arrows divide the diameter difference into a horizontal difference (*difference in number of rings = dnr*) and a vertical difference (*actual diameter difference = aDd*) as indicated by the green line. The grey vertical dashed line indicates the time of harvesting between 1956/58.

To investigate the behaviour of differences between twin cores over time, diameter and basal area differences were calculated for the years 1962, 1976, 1984 and 2005.

2.2.7. Gleichläufigkeit

To compare the similarity of twin cores of the same tree, their growths trends were analysed using the Gleichläufigkeit approach described by Eckstein & Bauch (1969) and Schweingruber (1988). This approach compares the increment trends of two cores for each year in comparison to the previous year. When the increment in one core increased from one year to the next, it was given the value 0.5 for that interval, when the increment was the same in two consecutive years, the value was 0 and when the increment decreased between two year, the value was -0.5 based on equation [5].

$$\Delta_i = (x_{i+1} - x_i) \quad when \quad \begin{array}{l} \Delta_i > 0 : G_{ix} = +½ \\ \Delta_i = 0 : G_{ix} = 0 \\ \Delta_i < 0 : G_{ix} = -½ \end{array} \qquad (5)$$

where x is the increment of a core in year i and G_{ix} is the assigned individual score depending on the relationship between x_{i+1} and x_i.

The scores for G_{ix} and G_{iy} in the interval i were then added up, resulting in a Gleichläufigkeit (G_v) value for that interval [equation 6], which can obtain values of either 0, 0.5 or 1. The summation of all G_v's returns a value that is converted into the proportion of the maximum possible value of Gleichläufigkeit.

$$G_{xy} = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| G_{ix} + G_{iy} \right| \qquad (6)$$

where G_{ix} and G_{iy} are the individual Gleichläufigkeit values for each tree core in an interval i and G_{xy} is the Gleichläufigkeit between the two cores over the whole period.

The example in Figure 9 is based on the comparison of two increment cores G_{ix} and G_{iy} of the Twin core study within a period of 10 years. The summation of all individual Gleichläufigkeit values returns the value 7.5 out of a maximum of 10 and therefore translates into a Gleichläufigkeit G_{xy} of 0.75 (75 %). The value for G_{xy} can be between 0 and 1, where the lowest value indicates that the increment trends of two cores do not match at all and the highest value indicates that the trends match perfectly. In the given situation of two cores taken from the same tree at the same height, the expected similarity is very high if the assumptions of age and increment core studies are met. The Gleichläufigkeit values were calculated using the Dendrochronology Program Library in R (dplR) 1.6.4 and the glk function (Bunn et al., 2017).

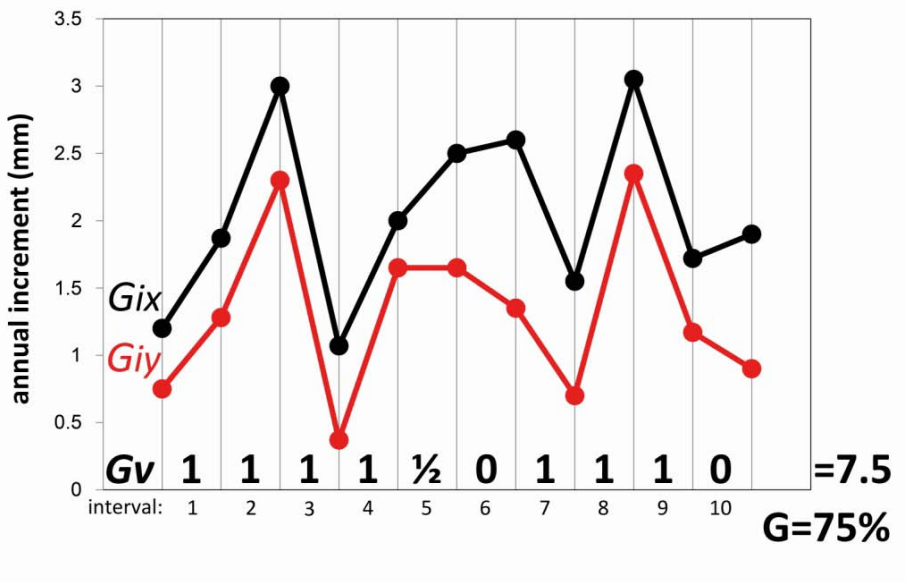

Figure 9. Comparison of the increments of two cores G_{ix} and G_{iy} of the same tree (twin cores) over a period of 10 years following the Gleichläufigkeit approach. *Gv*'s are the Gleichläufigkeit values for each compared interval and G is the resulted Gleichläufigkeit.

2.2.8. Release

Frequent annual changes of narrow and wide rings often indicate general phases of slow and fast growth (Schweingruber, 1993), that are related to environmental factors such as light, water or temperature. Abrupt changes in the light environment can induce a rapid growth response of individual trees, in particular for light-demanding tree species. When these changes can be related to particular events in time, they can be used for calibration purposes.

Such typical events in managed forest are harvesting and thinning, where individual trees are removed to reduce competition between trees. These silvicultural operations enhance the growth of residual trees and result generally in a rapid increase of annual ring width. Such a 'release' can often be identified visually (Schweingruber, 1988) but it can also be quantified by comparing the individual growth increment within a given year with the annual mean increment of previous years and with the annual mean increment of following years. Figure 10 shows the comparison of the annual mean increment of the past 10 years with the one of the following 10 years in a 225 yr old *B. tawa*. A release or changepoint can be seen in

1962 where the increase of the mean annual growth is > 25 %. This release coincides with selective logging in 1961 which led to a change in the light environment of the forest.

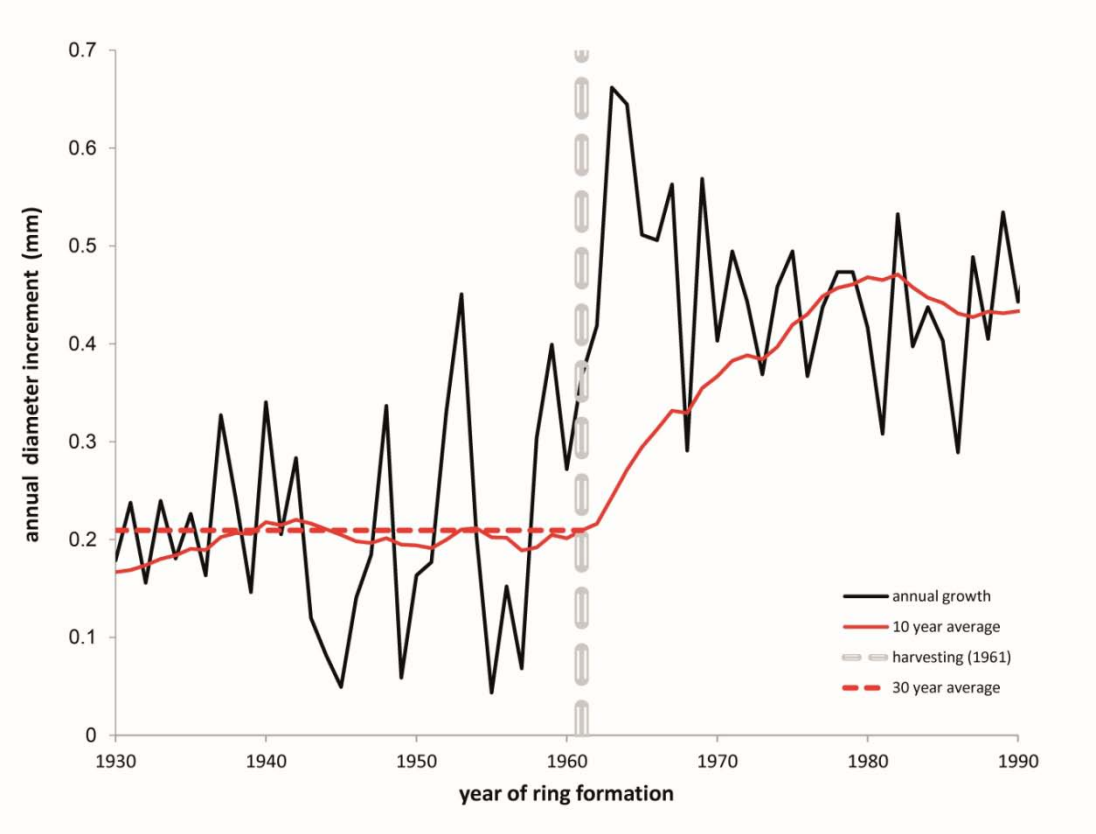

Figure 10. Definition of a growth release based on a comparison of the mean increment of the past 10 years and the mean increment of the following 10 years as seen in a 225 yr old *Beilschmiedia tawa* (dbh 43.8 cm).

Instead of using only the mean growth, the variance of growth can also be used as an indicator for release events. For the changepoint analysis in this study, multiple changepoints were detected using changes of the mean as well as changes of the variance as described by Killick et al. (2012) and with the help of the 'Changepoint' R-package (Killick & Eckley, 2013). This method allowed accounting for overfitting by applying a penalty value that depended on the individual growth patterns of *B. tawa* with a large year to year variation in growth. Figure 11 shows the results of this multiple changepoint analysis for the same tree portrayed in Figure 10 with corresponding release dates.

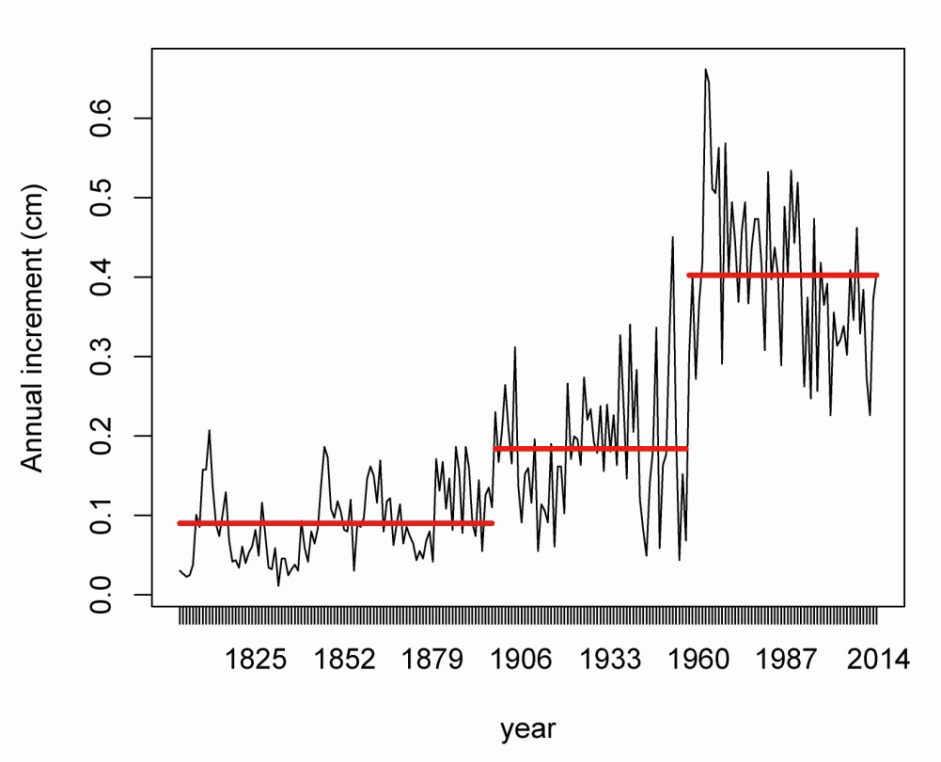

Figure 11. Changepoint analysis detecting changes in the variance and mean growth of a 225yr old *Beilschmiedia tawa* in 1898 and in 1962, one year after harvesting

As the exact year of harvesting was known, the release was used to calibrate the age estimates based on tree cores (Figure 12). The effect of false or missing rings could be estimated if they did not occur within the same period after harvesting, even though a delayed response from individual trees after a period of suppressed growth can add uncertainties.

Figure 12. Diameter growth release visible in a *Beilschmiedia tawa* tree core after harvesting in 1956/58

Based on the annual increment per year and the modelled bark diameter, a tree`s diameter was calculated for each year of its life. In the CP-study, these values were then compared to the measured diameters of the years between 1960 and 2005. The differences between estimated and measured diameters (*Diameter difference = Dd*) were used as one indicator for the suitability of increment cores to estimate the annual increments of trees for given periods.

2.2.9. Statistical modelling

All statistics were performed using RStudio 0.99.879. A One-way analysis of variance (ANOVA) was used to investigate if trees of all social classes showed the same relationship between measured and calculated diameters. The social class of a tree was recorded at the time of coring. But this does not necessarily mean that a tree belonged to the same social class in each of the years when measurements were taken. Over the past 54 years it could be expected that there was a shift in dominance of some trees. Some predominant (class 1) and dominant (class 2) trees might have died (old age, windthrow), giving way to former codominant (class 3) trees that grew into a higher social class. It could also be expected, that trees moved into lower social classes due to age (senescence, die back) or damage (crown damage, wind). The annual mean increment was tested as the second explanatory variable. Slower growing trees were expected to form narrower growth rings and faster growing trees forming wider rings. Both growth forms were suggested to influence a difference between calculated and measured diameters.

The third variable tested was the time that elapsed since the measurements. Even though the presence/ absence of false rings was to that point unknown and age estimations might not be exact, with the number of rings it was nevertheless possible to differentiate between young and old trees. It was assumed that trees of different ages show different growth patterns which might influence the *Dd* value.

A linear mixed effects model with maximum likelihood method (Pinheiro & Bates, 2002) as promoted by Bolker et al. (2008) was used to describe the relationship between measured and modelled basal areas for 86 time series from repeated dbh measurements between

1960 and 2014. This model was selected due to the hierarchical data structure and the differences in the number of measurements for the individual trees. The measured and converted basal areas were used as response variables. Levels of nesting were plot level (16 plots) and tree level (86 trees) and were set as random effects. The modelled basal areas (*mba*), mean basal increment (*mbi*) and number of years since measurements (*ysm*) were set as fixed effects. To ensure maximum flexibility, random intercepts and random slopes were used for each individual time series. The relationship between the fixed effects of the final model (predicted values) and the measured values (response) was then analysed further using a linear model, to describe the predictability of the calculated basal area based on increment cores on a stand level.

2.3. Results

2.3.1. Bark thickness

Analysis of 371 bark measurements of trees with diameters between 3.2 cm and 77 cm showed a strong positive correlation between the diameters of *B. tawa* trees and their bark thickness (Figure 13). With every 10 cm of diameter increment, the bark thickness increased on average by 1 mm. But bark thickness was not consistent along a measured circumference. Twin core bark measurements of 40 trees were found to differ by up to 61 % (μ = 20.1 ± 2.44) (Figure 14).

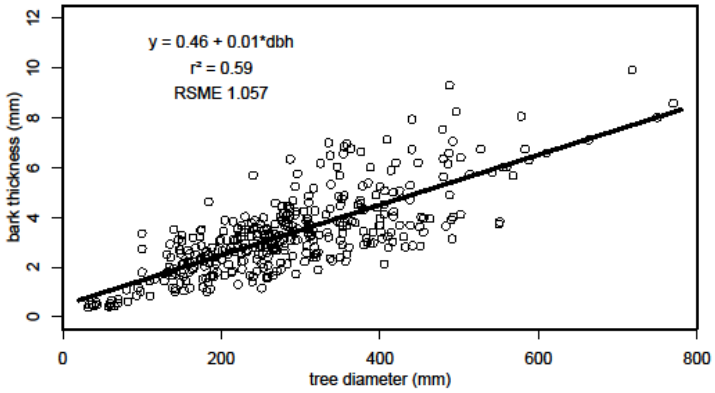

Figure 13. Relationship between bark thickness and tree diameter of *Beilschmiedia tawa* in a podocarp-broadleaved forest in the Central North Island of New Zealand (n = 371), dotted line = prediction

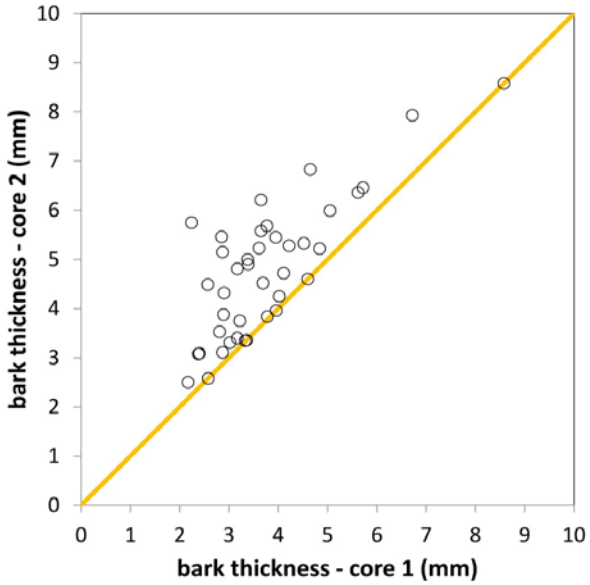

Figure 14. Relationship of twin core bark measurements of the same tree in 1.4 m height, n = 40 trees; the orange line shows the relationship where bark measurement of both cores of the same tree are equal

2.3.2. Difference between measured and calculated values – CP study

Based on the increment cores, diameters were calculated in the CP study for every tree and for every year of its lifespan as seen in the calculated growth curve of a dominant *B. tawa* with a 2014 dbh of 56.8 cm (Figure 15). The tree shows a steady growth without any obvious times of suppression or release over the past 265 years. The increment core was taken in a height of 1.4 m, and no information is available for the time it took the tree to reach coring height. A comparison between the calculated and the measured diameters (*Diameter difference = Dd*) of 1960, 1984 and 2005 for this tree shows an increasing difference over time from 0.53 cm/+0.97 % (2005) to 0.73 cm/+1.44 % (1984) and 1.41 cm/+3.03 % (1961) (Figure 16). This pattern of increasing difference over time was a general trend for all 86 cored trees (Figure 17). The mean difference between the measurements in 1962 and the corresponding calculated diameters was 2.16 cm (SE=0.19, SD=1.68, absolute values) or 23.86 % (relative difference) with a minimum of 0.01 cm and a maximum of 7.98 cm. In relative terms, the smallest difference was 0.08 % of the measured diameter and the largest difference 180.68 %. The mean difference decreased to 1.93 cm (1976), 1.50 cm (1984) and 0.52 cm (2005).

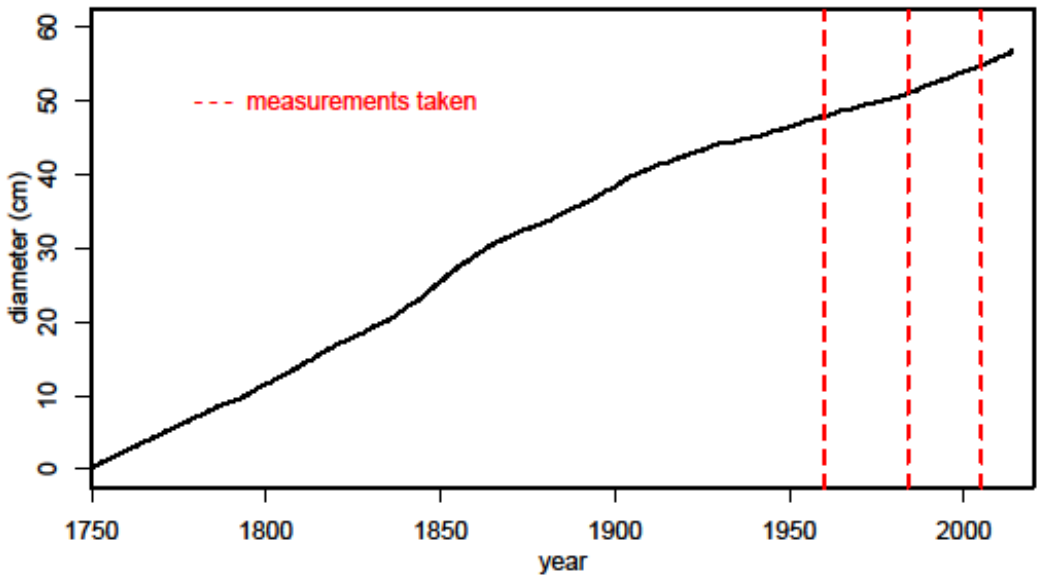

Figure 15. Calculated dbh for each year in the life of a 265-year old dominant *B. tawa* with dbh measurements taken in 1960, 1984 and 2005

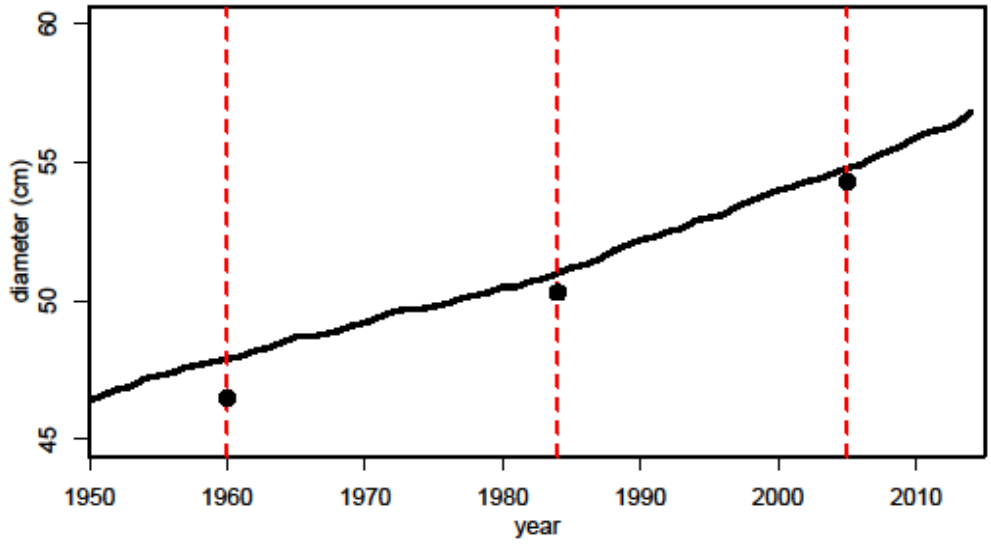

Figure 16. Difference of calculated diameters (black line) and measured diameters (black points) of a 265-year old dominant *B. tawa* in 1960, 1984 and 2005

Similar results are shown in the differences of calculated basal areas based on repeated measurements and tree cores (*Bad*) (Figure 18). The mean difference per tree was found to be 62.51 cm² (SE=7.70, SD=68.43, absolute values) in 52 years accounting for a relative difference of 27.49 %. Minimum (0.20 cm²) and maximum values (322.45 cm²) showed a large spread in those differences.

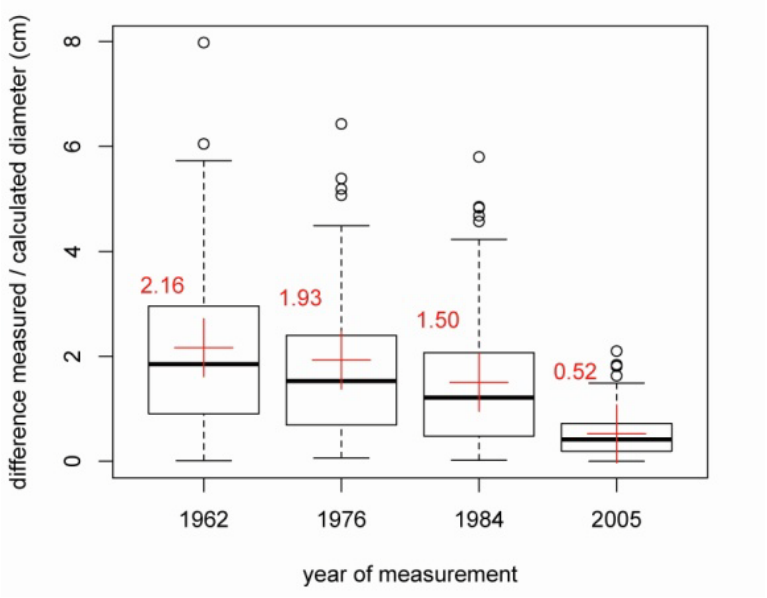

Figure 17. Increasing difference between measured and calculated diameters over time in 1962, 1976, 1984 and 2005 for 86 *B. tawa* (red crosses and values show means)

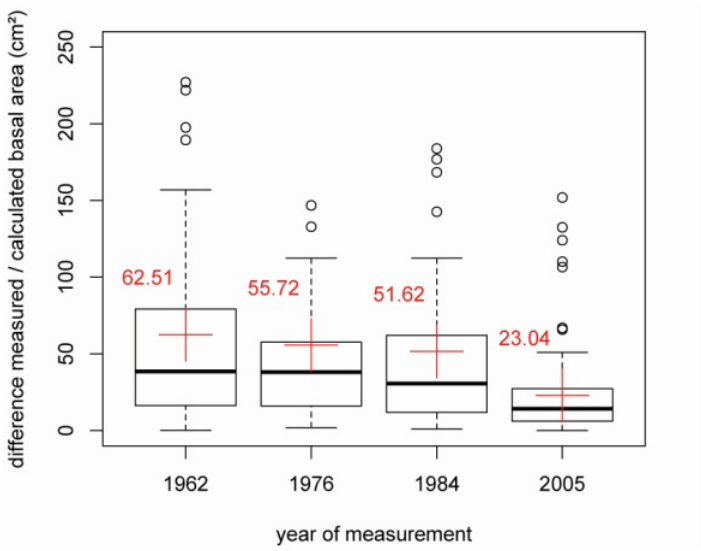

Figure 18. Increasing difference between measured and calculated basal areas over time in 1962, 1976, 1984 and 2005 for 86 *B. tawa* (red crosses and values show means) // visual y-axis coped at 250 cm²

The relative difference of calculated basal area increment between repeated measurements and tree cores was 27.22 % (SE=4.26, SD=37.63) with a minimum of 0.07 % and a maximum of 227.33 %. All trees (100 %) showed these differences at a varying magnitude with diameters being either over- or underestimated (Figure 19). But while the diameters of larger trees (dbh > 20 cm) were either over- or underestimated, smaller trees showed mainly an underestimation of the true (measured) diameters. The red line indicates an optimal *Dd* value of 0 cm (measured diameter = calculated diameter).

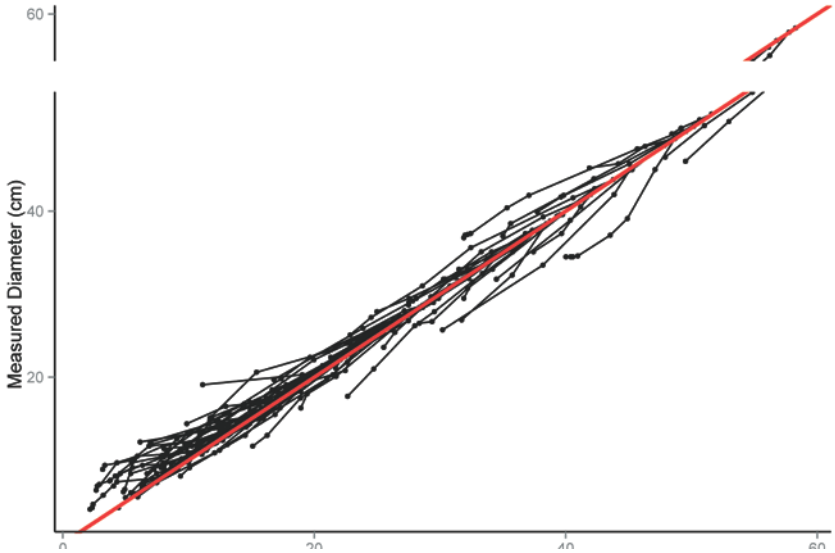

Figure 19. Relationship between calculated and measured diameters of 86 individual trees (1960-2014). The red line indicates values where calculated = measured diameters

2.3.3. Effect of Social Class

Trees of lower social classes were in general smaller trees. There was a strong relationship between social classes of trees and their diameters, with trees of more dominant classes having on average larger diameters (Figure 20). A simple one-way ANOVA returned significant p-values close to zero for all social classes (n = 86, F = 71.46, p < 0.001) and a tree with a smaller diameter belonged generally to a lower social class. But this correlation between social class and diameter could not be entirely related to a larger annual increment of dominant trees. The mean annual increment between 1960 and 2014 (Figure 21) returned significant p-values only for the classes 1, 2, 4 and 5 (Table 10).

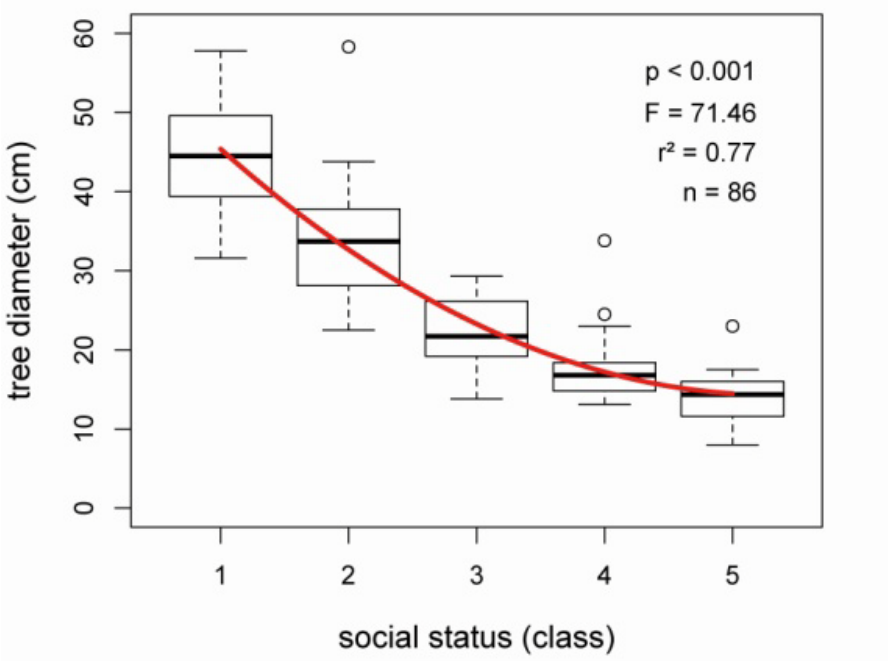

Figure 20. Relationship between the tree diameters and their corresponding social classes (trendline in red)

Table 10. One-way ANOVA results of the relationship of the *mean annual increments* (cm) of 79 *Beilschmiedia tawa* trees and their social status.

Period	Social class	t	*n*	df	F	R^2	*p*
1960-2014	1	12.203	79	74	17.15	0.453	< 0.001
	2	3.596					< 0.001
	3	-0.306					0.760
	4	-2.636					0.010
	5	-4.459					< 0.001

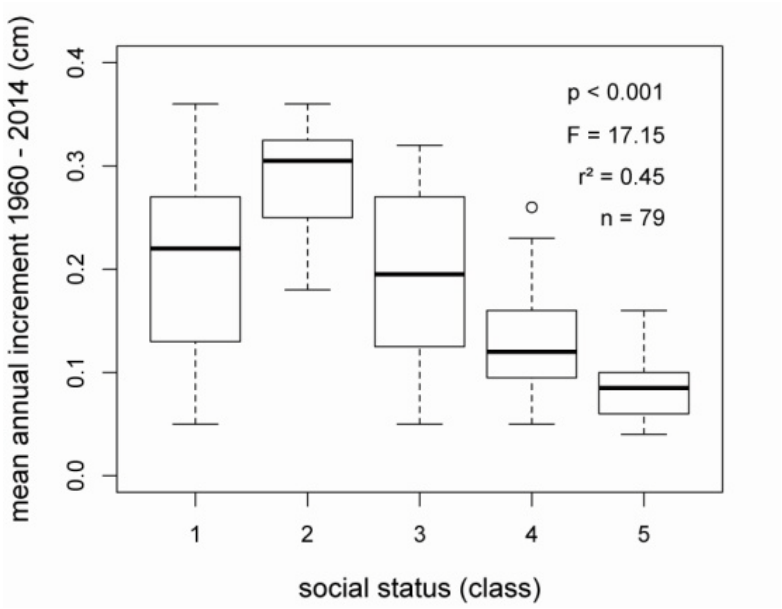

Figure 21. Relationship between the mean annual increment between 1960 and 2014 and their corresponding social classes

Results indeed showed a negative correlation between social class and *Dd* (Figure 22). The lower the social status of a tree was, the more likely was it, that *Dd* was negative. This means that the diameters of trees with lower social classes were more likely to be underestimated. This difference increased progressively over time.

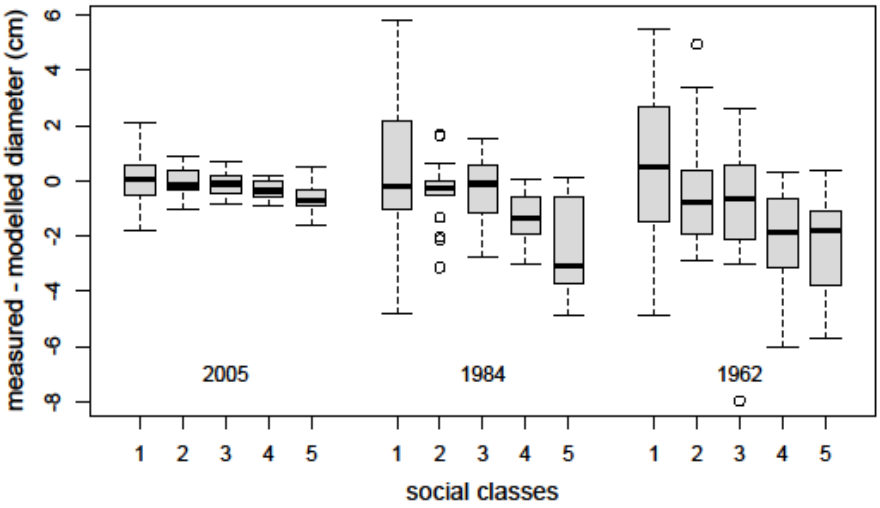

Figure 22. Effect of the social class of trees on the difference between calculated and measured diameters in 2005, 1984 and 1962 for 86 *Beilschmiedia tawa* trees

In particular, the values in the social classes 4 and 5 were significantly different from values for class 1 in the years 1984 and 1962. But even though this trend is clearly visible for the

mean difference, the variation in the response variable shows a low prediction value of the results (Table 11).

Table 11. Results of modelling the influence of social class on the difference between calculated and measured diameters in the years 2005, 1984 and 1962

Year	Social class	t	*n*	df	F	R^2	*p*
2005	1	0.301	86	81	2.631	0.0712	0.764
	2	-0.712					0.478
	3	-1.035					0.304
	4	-1.949					0.055
	5	-2.976					0.004
1984	1	1.202	84	79	7.422	0.2363	0.233
	2	-1.602					0.113
	3	-1.464					0.147
	4	-3.085					0.002
	5	-5.103					< 0.001
1962	1	1.144	79	74	4.845	0.1647	0.256
	2	-1.158					0.250
	3	-1.972					0.052
	4	-3.505					< 0.001
	5	-3.638					< 0.001

2.3.4. Variability of ring widths

The differences of ring widths between adjacent rings in increment cores of *B. tawa* were found to be extremely large. The analysis of 18,246 tree ring widths within the CP- and the Twin core studies showed a maximum difference between two consecutive rings of a factor 35.83 (Table 12). This means that this ring was 35.83 times wider than the previous or following ring. But even though these extremely large differences were rare, the mean difference was still of factor 2.14, which means that tree rings were on average more than twice as wide as their directly adjacent rings. However, the median of those values which is not affected as much by the extreme values as the mean, showed a factor of 1.57.

Table 12. Variability of distances between consecutive rings, where values are changes in factors form one ring to the following.

	n	mean	min	max	SD	SE	median
CP-study	13,020	2.19	1.00	35.83	1.91	0.016	1.60
Twin core	5,226	2.00	1.00	16.38	1.45	0.020	1.52
combined	18,246	2.14	1.00	35.83	1.79	0.013	1.57

This is even more visible in Figure 23, where 67.37 % of all tree rings (=> 12,293) were wider than their adjacent neighbours between factors of 1 and 2. Only 17.35 % (=> 3,166) of tree rings differed by factors 2-3 and 6.05 % (=> 1,269) by factors 3-4. The extreme differences between factors 10 and 36 accounted for only 1.25 % (=> 228) of the tree rings. Subdividing the factor classes 1 and 2 into 0.2 factor steps shows that 22.61 % (=> 4,125) of all tree rings were between 1 and 1.2 times wider than their neighbours (Figure 24). From there the widths differences decrease from one factor class to the next by c. 25 % per class until class 2.4 where the decrease slows down.

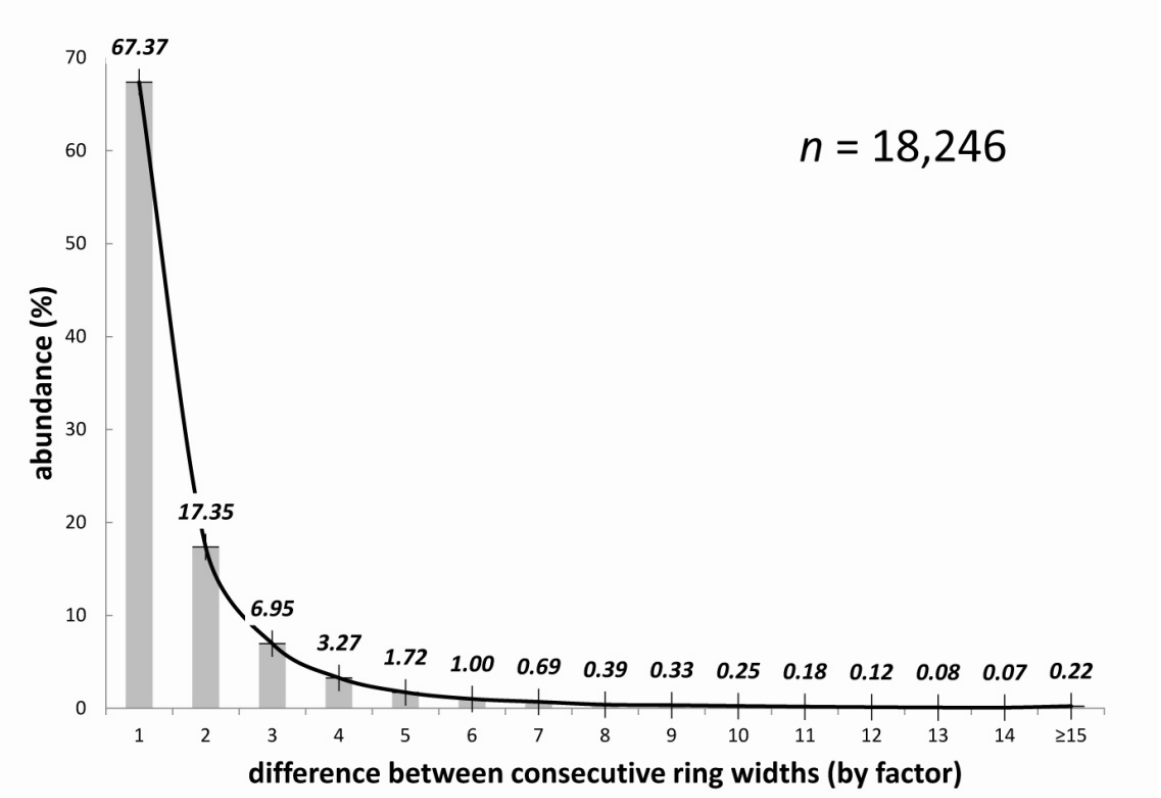

Figure 23. Variability of *B. tawa* tree rings widths as a factor of change between two consecutive rings. Here the abundance of tree rings in each factor class are shown.

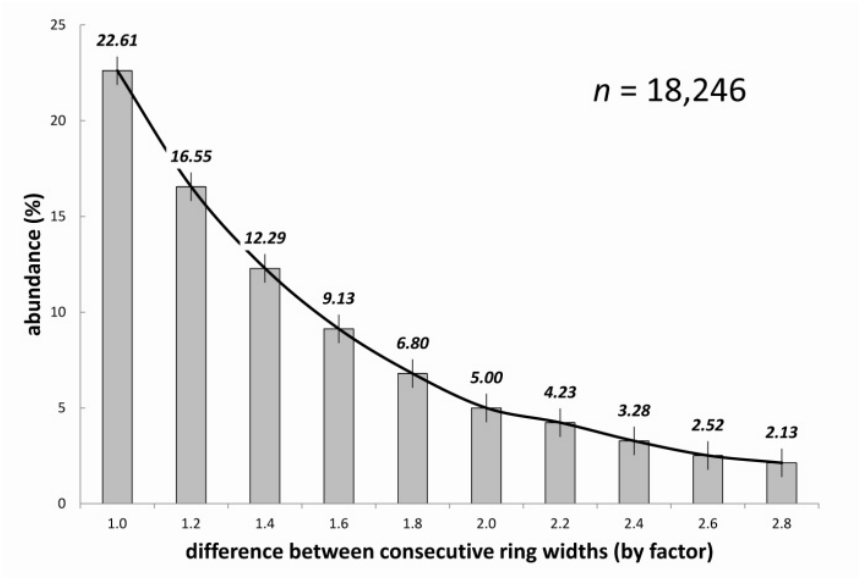

Figure 24. Variability of *B. tawa* tree rings widths as a factor of change between two consecutive rings. Here the abundance of tree rings is only shown for factor classes 1-2., (class names refer to the lower limit of the classes)

The spread in the values of the **mean sensitivity analysis** based on the widths of consecutive rings was between 0.3 and 0.9, covering almost the entire range of possible values. 82.5 % of all trees (=> 104 cores) had values between 0.4 and 0.65 (Figure 25), 42.8 % of the values (=> 54) were found to be between 0.5 and 0.6 and only 4.8 % of all tree cores (=> 6) showed values lower than 0.4.

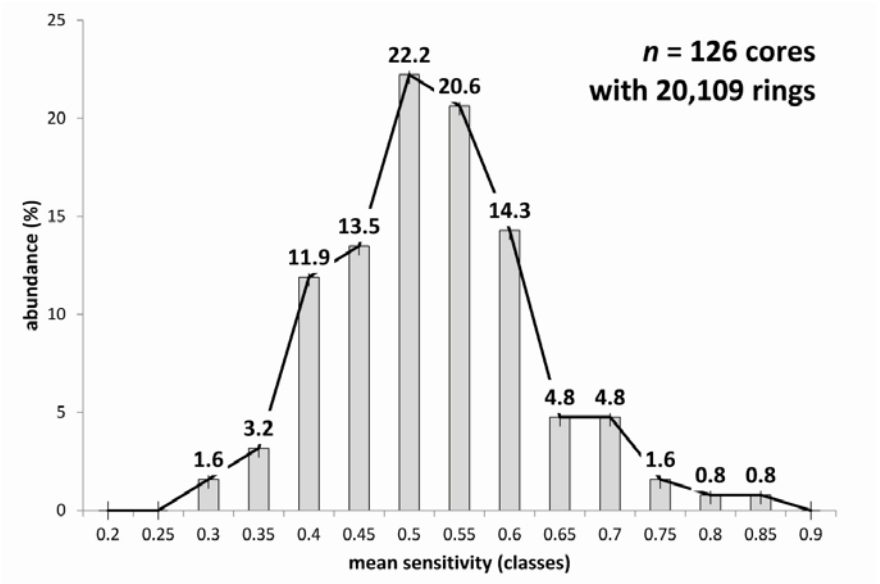

Figure 25. Results of a mean sensitivity analysis showing the variation of consecutive *B. tawa* tree ring widths, where class names refer to the lower limit of each class.

Standard regression methods showed no significant relationship between the mean sensitivities and the number of rings (p = 0.55, RSE = 0.099, F = 0.37), the estimated age (p =

0.57, RSE = 0.99, F = 0.33) and the social class of trees (p = 0.37, RSE = 0.099, F = 1.08). A weak correlation was found between the mean sensitivities and the diameter of trees (p = 0.03, r^2 = 0.06, RSE = 0.096, F = 9.15) and a strong correlation between the mean sensitivities and the mean annual increments (*mai*) of trees (p < 0.0001, RSE = 0.089, F = 18.07). The larger the increment of trees was the more likely was it that they showed a lower mean sensitivity. But the spread in the data was large and the model explained only 12.18 % of the variation.

2.3.5. Difference between two cores of the same tree – Twin core study

The comparison of calculated diameters of 40 twin core pairs with 5065 annual ring widths measurements covered a maximum span of 257 years (Twin core study). The results show that 95.75 % of the calculated diameters based on twin cores did not match (Figure 26). And only 3.16 % of all twin core diameters matched when recent values between 2004 and 2014 were discarded. Diameter differences were well balanced between over- and underestimation. The mean diameter difference was 1.21 cm (SE = 0.01, SD = 1.05) with a maximum of 5.80 cm in comparison to the mean diameter difference of 1.45 cm (SE = 0.08, SD=1.46) in the CP-study with a maximum of 7.98 cm.

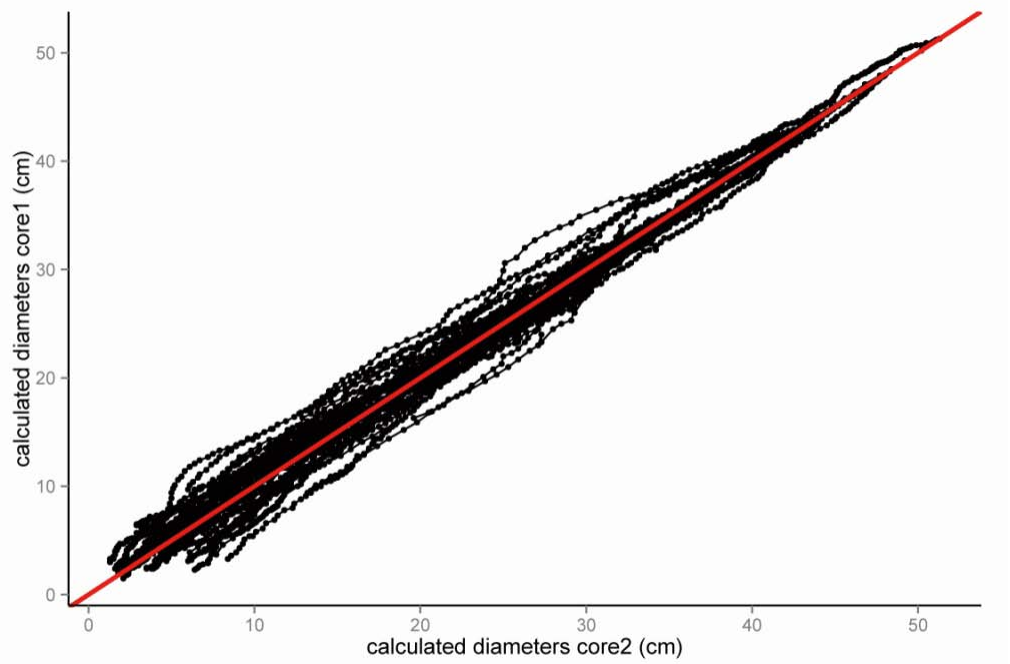

Figure 26. Relationship between diameters calculated on the basis of pairs of two cores taken from the same tree at the same height (twin cores), n = 40 trees, the red line indicates values where core 1 = core 2

While the diameter difference steadily increased over time in the CP-study, this was not as clearly visible in the Twin core study (Figure 27). Mean difference in 1962 was 1.36 cm (SE=0.17, SD=1.05, absolute values) or 7.61 % of the diameters of core 2 (relative difference) with a minimum of 0.03 cm and a maximum of 3.98 cm. The smallest difference was 0.14 % of the calculated diameter of core 2 and the largest difference 28.29 %. The mean differences for the other years were 1.20 cm (1976, min = 0.03 cm, max = 3.63 cm), 1.22 cm (1984, min = 0.004 cm, max = 5.53 cm) and 0.41 cm (2005, min = 0.01 cm, max = 1.57 cm).

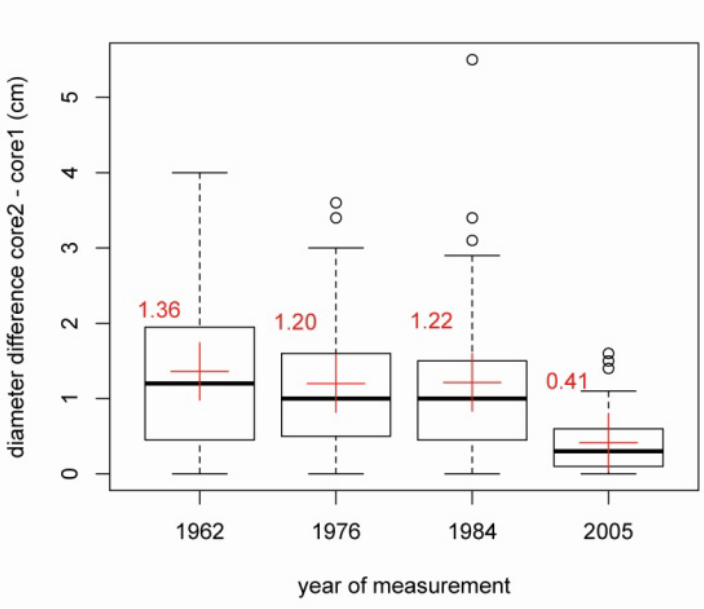

Figure 27. Diameter difference between two cores of the same tree (twin cores) over time in 1962, 1976, 1984 and 2005 for 40 B. tawa (red crosses and values show means)

Converting those differences into basal area terms showed a difference similar to the CP study (Figure 28). The mean difference for 1962 was 43.84 cm² (SE = 5.65, SD = 35.30) accounting for a relative difference of 15.37 % of the basal area calculated for core 2. The minimum was 1.08 cm² and the maximum 157.30 cm². Differences for values in 1976 (mean = 51.13 cm², SE = 6.24, SD = 38.99, min = 1.11 cm², max = 149.39 cm²) and 1984 (mean = 57.63 cm², SE = 8.99, SD = 56.11, min = 0.13 cm², max = 270.74 cm²) were even higher. The differences for 2005 (mean = 24.20 cm², SE = 4.21, SD = 26.29, min = 0.87 cm², max = 100.11 cm²) were again very similar to the ones in the CP study.

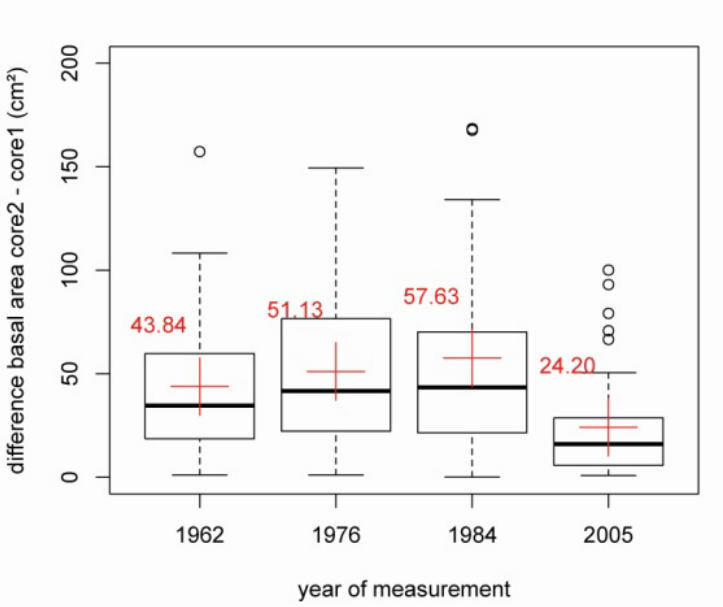

Figure 28. Difference between calculated basal areas of twin cores over time in 1962, 1976, 1984 and 2005 for 40 B. tawa (red crosses and values show means)

2.3.6. Gleichläufigkeit

The analysis of the similarity of 10,612 growth trends of 40 twin cores pairs (core 1 vs. core 2) showed an unexpectedly low mean of 0.55 (±0.039, SE = 0.019, SD = 0.12, median = 0.52) with an interquartile range from 0.47 to 0.58. This means that growth patterns of 2 cores taken from the same tree at the same height with a horizontal offset of 90° did not match (Figure 29). After accounting for the number of false and missing rings, new diameters and annual increments were calculated for core 1 and the Gleichläufigkeit analysis was carried out again (core 1co vs. core 2). The mean Gleichläufigkeit improved by 0.21 to 0.76 (±0.036, SE = 0.018 , SD = 0.11, median = 0.80), which means that false and missing rings accounted for a mean Gleichläufigkeit difference of 39 %.

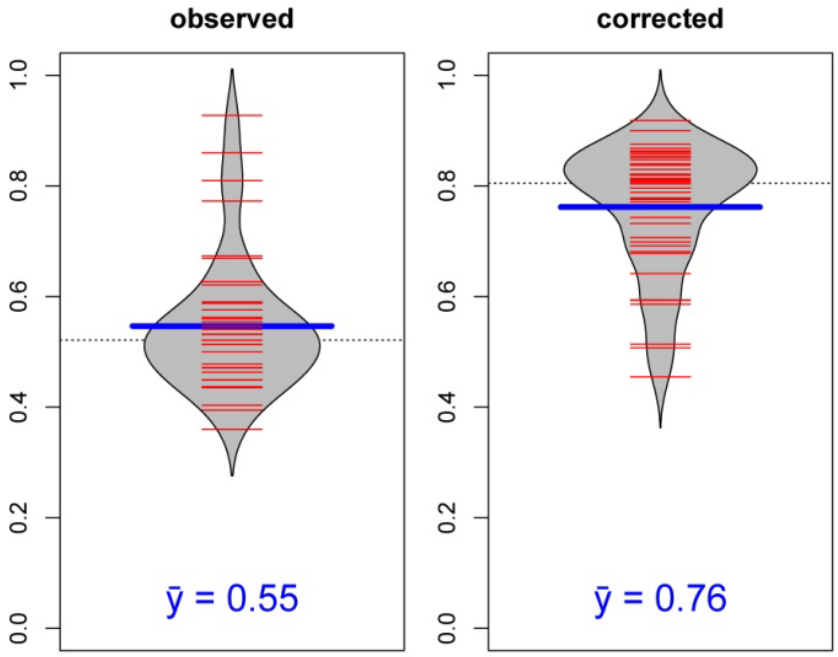

Figure 29. Gleichläufigkeit for 40 pairs of twin cores. The left plot shows the values for the direct comparison between twin cores (core 1 vs. core 2), whereas the right plot shows the values after accounting for false rings (core 1co vs. core 2). Distributions are plotted as density shapes with the mean line (blue) for the distribution. The dotted horizontal line is the overall average for the plot. The red "beanlines" are corresponding to the Gleichläufigkeit values for each pair of twin cores.

2.3.7. Effect of false and missing rings in age studies

Growth patterns visible in added increment curves of two cores of the same tree as well as release analysis showed that false / missing rings are a common feature in *B. tawa* (Figure 30). Comparisons between growth patterns of historically measured diameters in the years 1960-2014 and calculated diameters (based on single cores, n_1 = 40) showed that only 27.5 % (11 trees) of trees indicated no false or missing rings. The majority of trees (50 %, 20 trees) showed between 1 and 6 false/missing rings in 50 years and 10 % (4 trees) of trees showing between 7 and 11 false/missing rings. 12.5 % of trees (5 trees) showed more than 15 false/ missing rings, with 3 trees indicating between 22 and 32. Similar results are received by a comparison of two individual cores of the same tree (twin cores, n_2 = 40). Again, only 30 % (12 trees) of twin cores show no age difference. The majority of twin cores (62.5 %, 25 trees) show differences of 1 to 6 rings while 7.5 % of twin cores (3 trees) show differences between 7 and 15 rings in a period of 50 years.

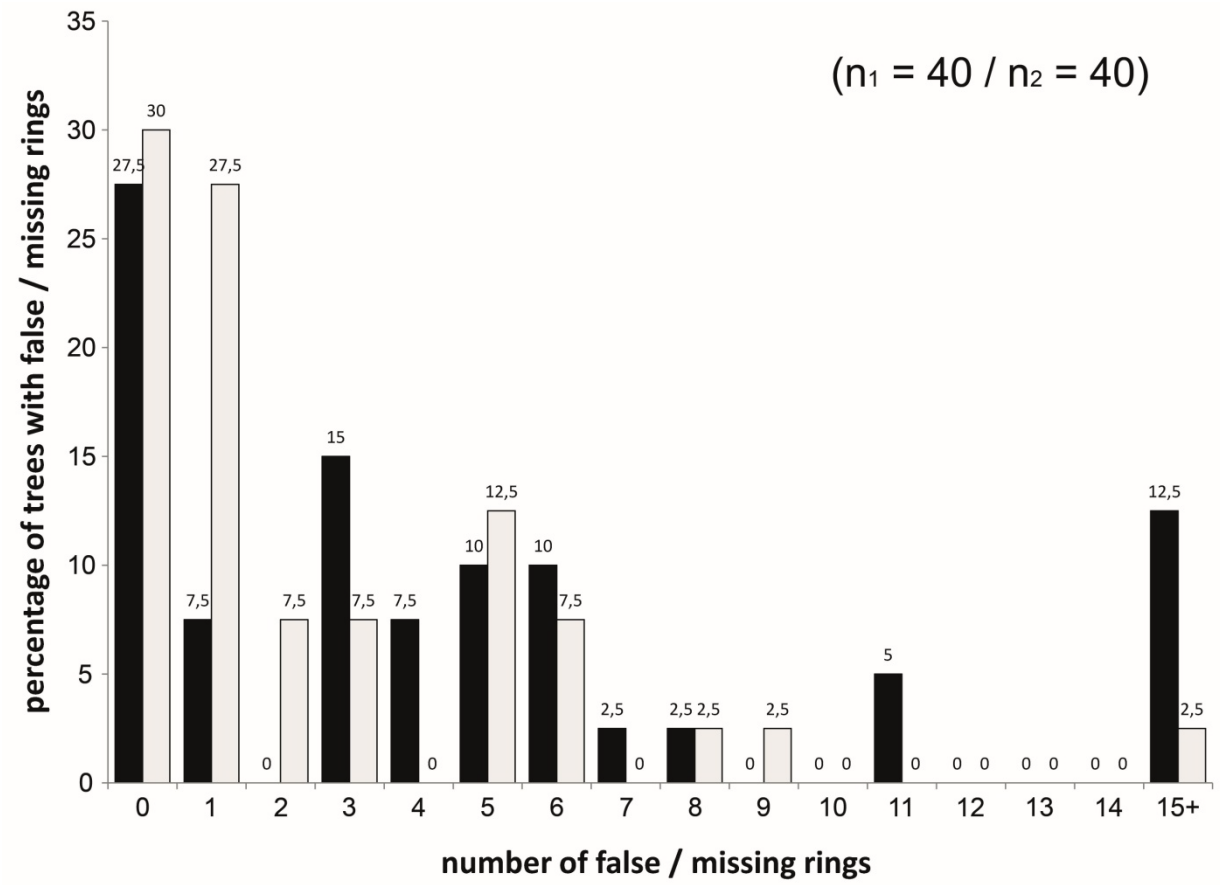

Figure 30. Percentage of trees that indicated missing or false rings within a period of 50 years from 1965-2014. Black bars indicate results based on comparisons of measured diameters vs. calculated diameters (based on tree cores, n_1 = 40), whereas grey bars indicate results based on the comparisons of 2 cores of the same tree (n_2 = 40).

These false and missing rings could not be related to any specific events in time but seemed to occur on a rather irregular basis throughout the lifespan of trees. Figure 31 shows a dominant (class 2) 172 year old *B. tawa* (dbh = 30.9 cm) where two cores taken at the same height differ by 9 rings in 105 years. This difference is highly visible at the time of release initiated by harvesting between 1956 and 58. In core 1 (black line) the release seems to have occurred 3 years before harvesting commenced in 1956 whereas in core 2 (red line), the release is visible in 1959, one year after the end of harvesting. Here, the difference of 5 rings in core 1 seems to reflect an overestimation of age caused by false rings in that core.

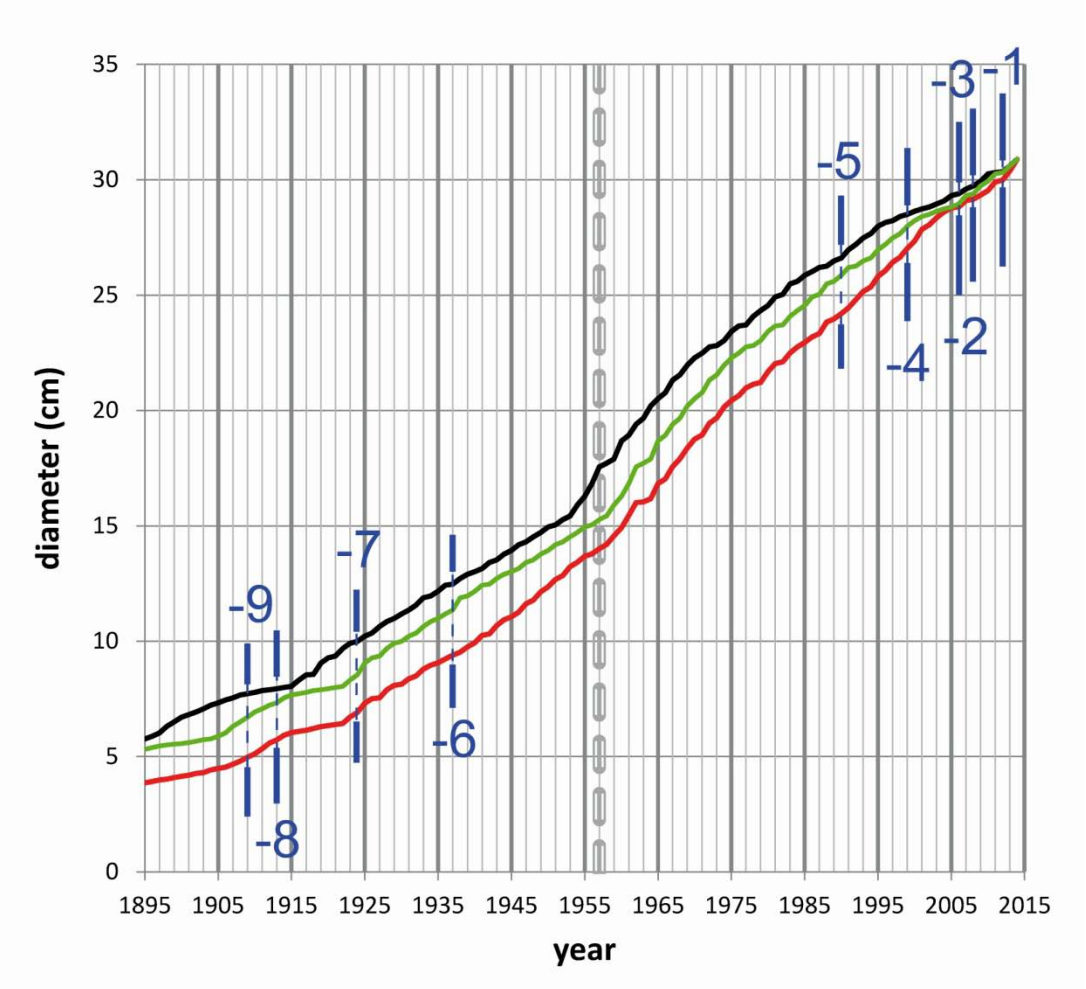

Figure 31. Increasing difference in the number of rings visible in two tree cores (core 1 = black line, core 2 = red line) taken at the same height from one *B. tawa* tree. Their age relationship (green line) is expressed as: core 1 + x = core 2, where x is the number shown in the diagram. The grey dashed vertical line indicates the time of harvesting in the years 1956-58.

By comparing twin cores of 40 trees over a time frame of 130 years, 185 false/missing rings were detected accounting for an average of 1.4 rings yr^{-1} (Figure 32). This means that their annual formation affected on average 4.2 % of all trees per year. However, there is a visible increase of false and missing rings in the past 30 years (2.9 rings yr^{-1}), meaning that the annual formation affected during that time on average 7.2 % of all trees per year and even 10 % in the past 15 years.

The number of false/missing rings was even higher when comparing growth patterns of 40 tree cores of the CP study over a period of 30 years (6.2 rings yr^{-1} with 15 % of trees affected per year), and as many as 7.7 rings yr^{-1} (18.7 % of trees) in the past 15 years.

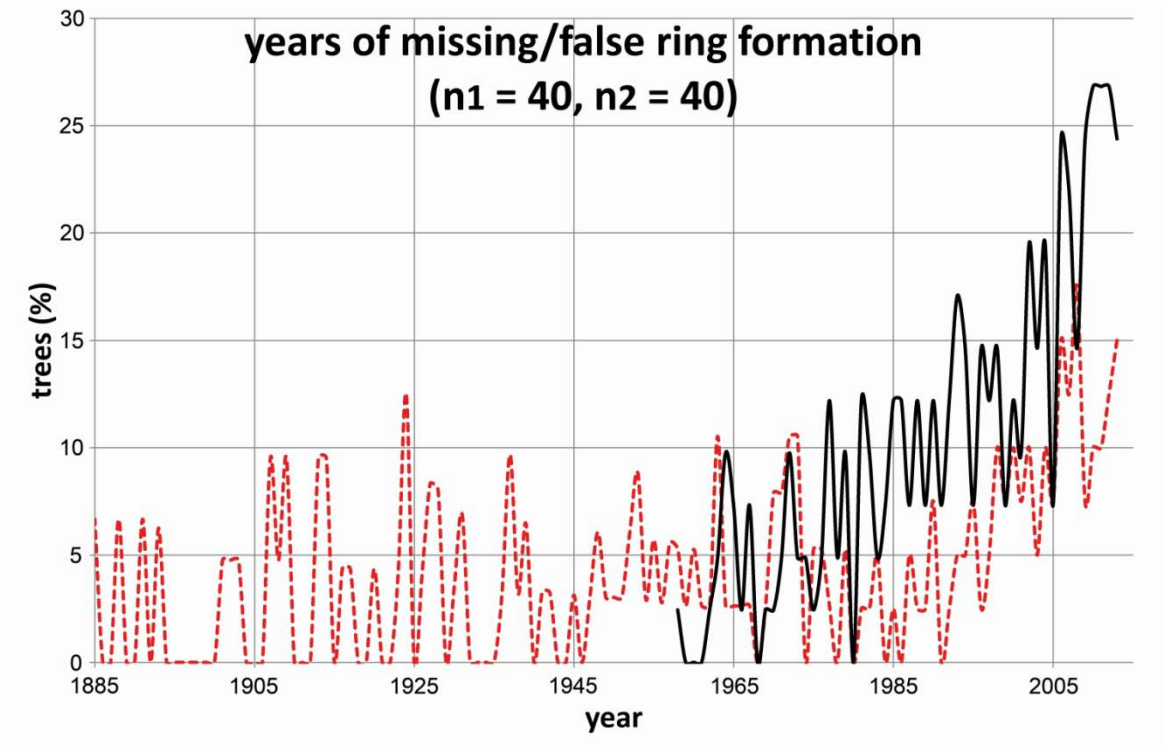

Figure 32. Percentage of trees that are affected by ring number differences (false/missing rings) between measured values and tree cores (CP-study = black line) as well as between two cores of the same tree (Twin core study = red dashed line) // n_1 = 40, n_2 = 40

2.3.8. Effect of false rings in increment studies

False rings not only lead to an over- or underestimation of age but also have a strong influence on the results of increment studies. Figure 33 shows a dominant *B. tawa* tree (dbh = 44.1 cm), where the number of false rings accounts for 82.7 % of the diameter difference between twin cores within the period from 1980 to 2014 (34 years). Accounting for false rings reduced the diameter difference from an average of 1.02 cm yr^{-1} (max. 2.4 cm) down to 0.18 cm yr^{-1}.

A similar result shows the comparison of the basal area, where false rings accounted for 83.1 % of the difference. Taking them into account reduced the average difference by 48.9 cm^2 from 58.9 cm^2 down to 9.9 cm^2 yr^{-1}. False rings also accounted for 80.5 % of the annual basal area increment difference in the 34-year period. Taking them into account reduced the annual average difference from 3.6 cm^2 by 2.9 cm^2 down to 0.7 cm^2 yr^{-1}.

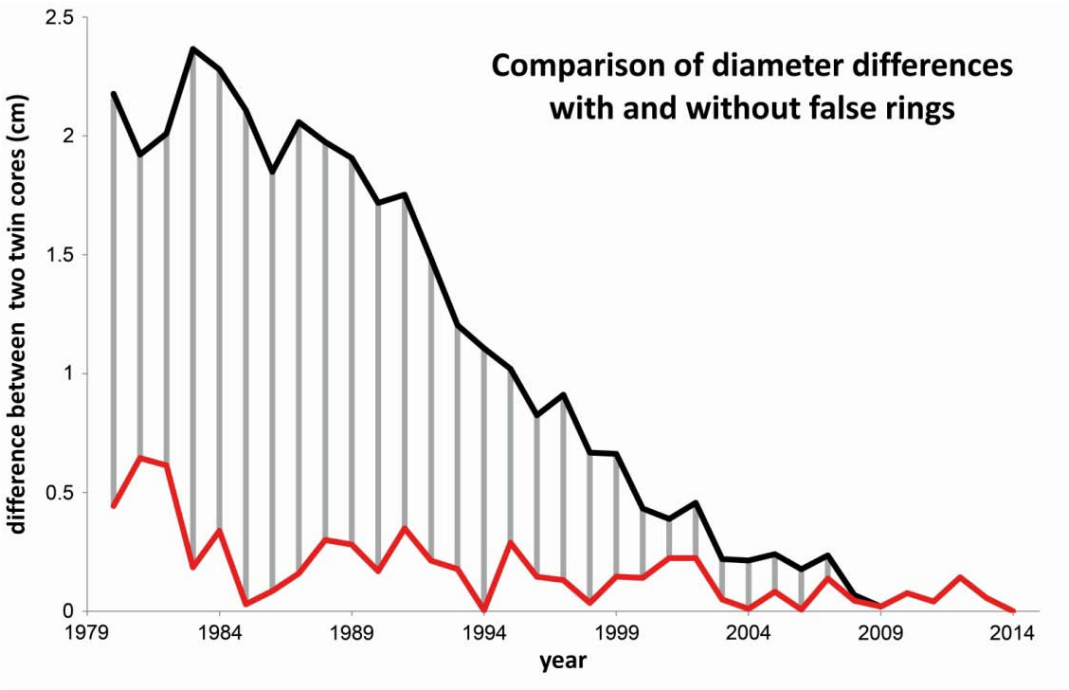

Figure 33. Example of the effect of false rings on the tree diameter difference between two cores of the same tree over a period of 35 years. The black line shows the diameter differences without taking the false/missing rings into account. The red line shows the diameter differences after subtracting the false/missing rings.

These strong effects of false and missing rings were observed in comparisons of measured and calculated values (CP study) as well as between twin cores of the same trees (Table 13). The annual basal area increments in the CP-study differed on average by 0.96 cm² yr^{-1} (min = 0.06 cm², max = 5.09 cm², median 0.59 cm²) and in the Twin core study by 0.97 cm² yr^{-1} (min = 0.02 cm², max = 4.81 cm², median = 0.70 cm²). Even though the effects of false and missing rings are different between the CP-study and the Twin core study, the unexplained difference in both studies is quite similar.

Table 13. Effects of false and missing rings and remaining unexplained differences for diameters, basal areas and annual basal area increments in the CP study and the Twin core study within 52 years between 1962 and 2014.

	mean	**false / missing rings**		**unexplained diff.**	
CP study		absolute	(%)	absolute	(%)
Diameter difference (cm)	1.96 ±0.50	1.18	60.2	0.78	39.8
Basal area difference (cm²)	51.85 ±21.9	30.74	59.3	21.10	40.7
Annual basal area increment difference (cm²)	1.00 ±0.42	0.45	44.6	0.55	55.4
Twin core study					
Diameter difference (cm)	1.36 ±0.33	0.60	43.8	0.76	56.2
Basal area difference (cm²)	43.84 ±11.1	18.37	41.9	25.47	58.1
Annual basal area increment difference (cm²)	0.97 ±0.31	0.34	35.4	0.63	74.6

Figure 34 shows the variation in the effects caused by false and missing rings where 60.2 % of the diameter difference between repeated measurements (1962-2014) and calculated diameters based on tree cores (2014) (CP-study) were a result of false and missing rings. For twin cores of the same tree (Twin Core study), false and missing rings still accounted for 43.8 % of the diameter difference.

This effect is very similar to the one observed in comparisons of basal areas, where 59.3 % of the differences in the CP study could be related to false and missing rings and 41.9 % of the difference in the Twin core study. In basal area increment terms, false and missing rings still account for 44.6 % of the difference in the CP study and 35.4 % in the Twin core study.

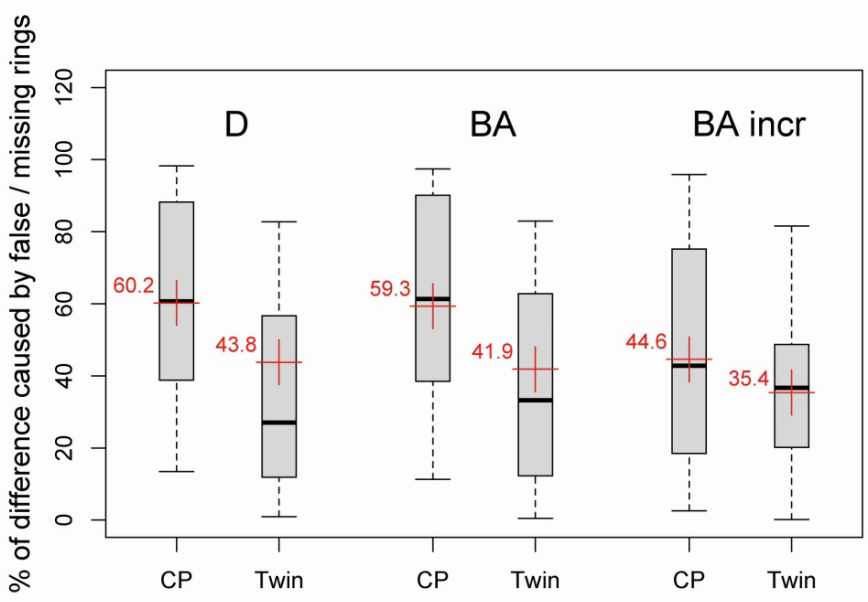

Figure 34. Percentage of differences in diameters (D), basal area (BA) and basal area increment (BA incr) caused by false/ missing rings detected in comparisons of measured and calculated values (CP, *n* = 30) as well as between twin cores (Twin, *n* = 36)

2.3.9. Relationship between missing / false rings and annual increment

Trees of different social classes in the CP-study were affected by diameter differences in different ways (Figure 22). The relationship between the mean annual increment (*mai*) of trees and their social status (Figure 21) lead up to the hypothesis that *mai* also has a significant relationship with the number of **missing rings**. A standard regression was used to evaluate this relationship for 40 trees of the CP-study within the observed span of 52 years (Figure 35). Of these, 24 trees (60 %) showed missing rings, while 6 trees (15 %) showed false

rings. 10 trees (25 %) showed no missing or false rings within that period. The relationship found was significant ($p < 0.0001$, $F = 49.07$, $r^2 = 0.55$, $n = 40$). Trees with more than 10 missing rings (20 %) in 52 years had an overall mean annual increment of 0.12 cm (min = 0.04 cm, max = 0.32 cm, median = 0.09 cm) and belonged in all cases but one (class 2) to the social class 5 (suppressed understorey trees).

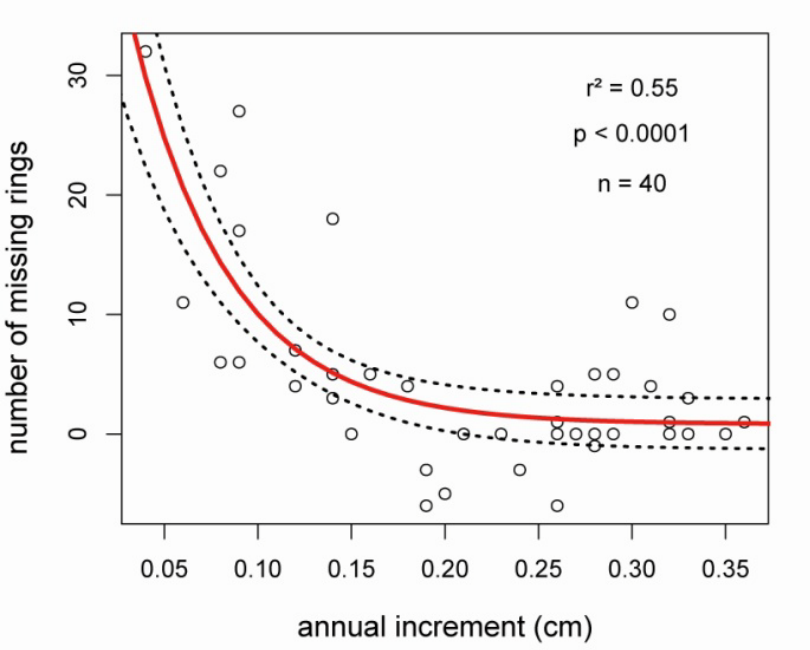

Figure 35. Relationship between annual increment and the number of missing rings within an observation time of 52 years (1962-2014) (CP-study)

The trees that showed **false rings** on the other hand had an overall mean annual increment of 0.22 cm (min = 0.19 cm, max = 0.28 cm) and belonged to the social classes 1 (predominant), 2 (dominant) and 3 (codominant). The average growth across all trees in the CP study was 0.21 cm (min = 0.04 cm, max = 0.36 cm).

The same analysis was carried out for the relationship between the calculated differences in the number of rings of twin cores and *mai* (Figure 36). But while the CP study covered trees of all social classes, trees for the Twin Core study were selected based on their diameter. To obtain as many ring measurements as possible, only the trees with the largest diameters were selected for this study. These trees belonged to the social classes 1 and 2 and had an overall mean annual increment of 0.32 cm (min = 0.11, max = 0.57 cm) in 52 years. Even though the trend in this relationship was similar ($p < 0.0001$, $F = 33.66$, $r^2 = 0.48$, $n = 35$), it was not as significant.

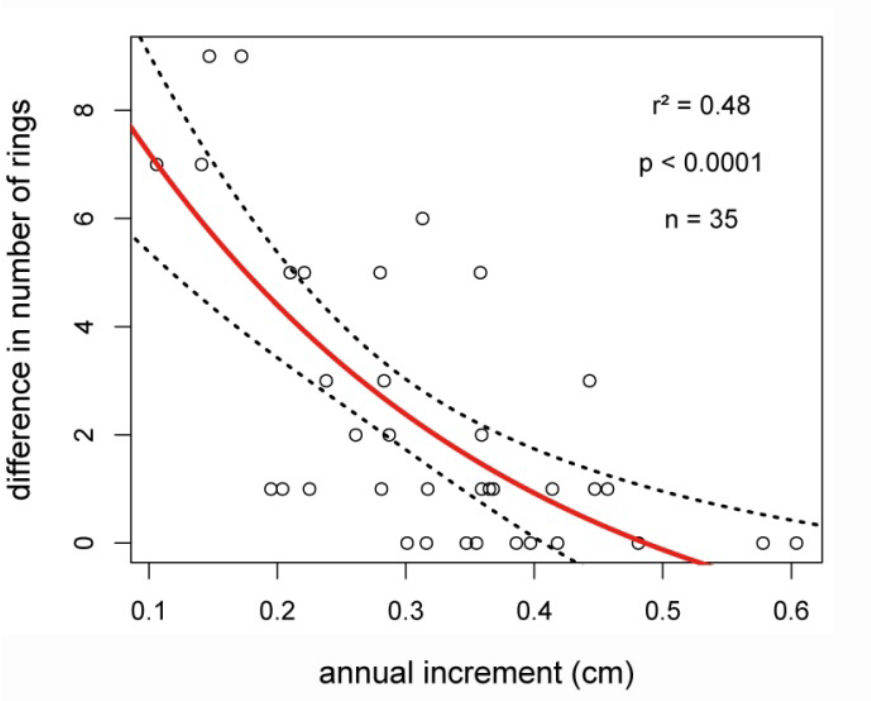

Figure 36. Relationship between annual increment and difference in the number of rings of twin cores within an observation time of 52 years (Twin core study)

2.3.10. Mixed effect modelling

Conversion of the radial diameters into basal area was used for mixed effects modelling and it was found that the calculated periodic mean annual increment since measurement (*pmai*) and time since measurement (*ysm*) were the most significant contributors explaining the difference between calculated and measured values (Table 14).

Table 14. Final mixed effects model showing the relationship between random and fixed effects (n=433)

Effect	Type	SD			
Random	intercept	6.33			
	time	1.76			
	residuals	20.36			
		value	**SE**	**t-value**	**p-value**
Fixed	intercept	1.145	3.043	0.376	0.706
	modelled basal area (*mba*)	0.998	0.003	300.219	< 0.0001
	mean annual increment (*mai*)	3.683	0.624	5.894	< 0.0001
	year since measurement (*ysm*)	0.470	0.346	1.355	0.176
	mba x *mai*	-0.002	< 0.001	-5.463	< 0.0001
	mba x *ysm*	-0.005	< 0.001	-8.837	< 0.0001
	mai x *ysm*	-0.188	0.041	-0.459	0.646
	mba x *mai* x *ysm*	<0.001	< 0.001	7.109	< 0.0001

The random effect 'plots' was found to be not significant but was left in the final model to maintain the model structure. Even though the effect for *ysm* was not significant in the final model, this model showed the best fit of all tested models based on an AIC and log-likelihood comparison. And due to the principle of marginality they were left in the model as two interaction terms of this variable were highly significant. Even though the residuals were large, they were evenly distributed and indicated linearity.

2.3.11. Model testing

Focussing on the fixed effects of the mixed effects model revealed the relationship between the mean of the modelled basal areas and the mean of the calculated basal area of this population of trees (Figure 37). This relationship was found to be highly significant (F = 3.717e+05, R^2 = 0.9988). The confidence intervals of the model showed that there was more uncertainty around the intercept (97.5 % CI [-2.504, 2.225]) than around the slope (97.5 % CI [0.997, 1.003]).

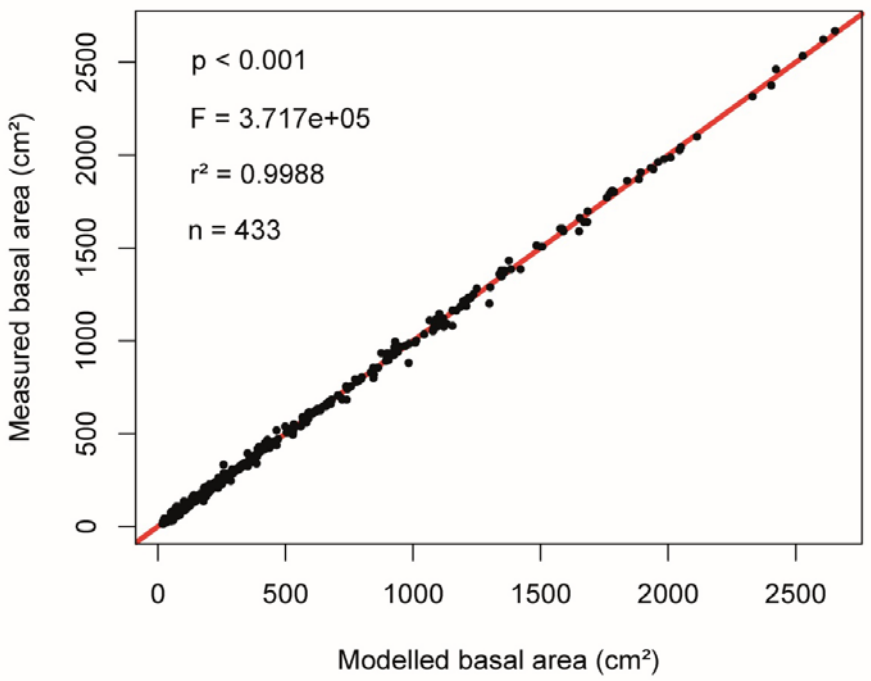

Figure 37. Relationship between modelled and measured basal areas of 86 *B. tawa* trees (1960-2014). The red line reflects values where measured basal areas equal modelled basal areas.

2.4. Discussion

2.4.1. Bark thickness

The observed positive relationship between **bark thickness** and tree diameter was significant (n = 371, p < 0.0001, s = 1.057, r^2 = 0.59) even though bark thickness could vary by up to 46 % along different radii. The increase of bark thickness with tree diameter is in line with findings of Richardson et al. (2015) who analysed the thicknesses of 125 *B. tawa* trees that were measured across New Zealand by Landcare Research with diameters between 2.1 cm and 62.3 cm. But the mean relative bark thickness as a percentage of diameter was at Pureora only 1.21 % and with that 42 % lower than the mean relative bark thickness of 2.1 % in the Landcare Research data set. In particular, smaller diameter trees had much thinner bark at Pureora than at other sites. It was suggested that the community-weighted mean (*cwm*) bark thickness could be related to nutrient levels in soil, but Richardson et al. (2015) did not find a correlation between *cwm* and soil C:N or soil total P. An attempt to link bark thickness and fire resistance in New Zealand temperate rain forests, where a mean relative bark thickness of 2.3 % was calculated for *B. tawa*, also failed (Lawes et al., 2014). However, Richardson et al. (2015) found a correlation between *cwm* and climate variables such as minimum temperature (r^2 = 0.02) and the ratio of total rainfall to potential evapotranspiration (r^2 = 0.08). But whether this is related to the low bark thickness of *B. tawa* at Pureora or to genetic features remains to be tested.

2.4.2. Counted variables

In addition to core measurements, the observed **numbers of rings** differed significantly in both studies. In an observed period of 50 years, only 27.5 % of the trees in the CP-study had matching numbers of rings and only 30 % in the Twin core study. False and missing rings accounted for observed errors between 2 and 12 % (1-6 years) in that period. But even when the total number of rings in one tree matched, growth patterns in twin cores showed that numbers of rings can vary with cores showing fewer rings than their twins in one decade but more rings in another decade. Over a longer period they counterbalanced each other.

These findings are in contrast to observations made by Ogden & West (1981), who found 19 clear and complete growth rings in discs of 8 trees that were felled 19 years after harvesting. These trees were repeatedly measured since 1961 and when felled, diameters ranged from 5.3 cm to 43.0 cm. They were estimated to be between 77 and 102 years old and seem to have covered all social classes. Diameter increments matched closely between the historical measurements and the disc analysis. Therefore they concluded that ring formation in *B. tawa* was annual, even though they confined their findings to fast growing trees. Large old trees as well as suppressed understorey trees though were found to show eccentric and lobate growth which makes age determination more difficult (Ogden & C. J. West, 1981). On the other hand, Dunwiddie (1979) found ambiguous parenchyma bands as well as lobate growth prominent in *B. tawa*. In a study reported by Knowles & Beveridge (1982), four *B. tawa* that were felled in 1968 at Kohuratahi, Taranaki, and of which dbh measurements were recorded over the previous 40 years, showed a strong correlation between the numbers of parenchyma bands and annual growth with 0.93 bands yr^{-1} in tree discs. While in slower- and faster growing trees normally one band was produced in each year, they also observed years where no band or even two bands were found. Unfortunately, those studies analysed only very small numbers of trees and their findings can therefore not be generalized.

In this study, the increase and decrease of the difference in numbers of rings seemed to be related to certain events in time. While in some periods over the past 130 years no increase of the difference in the numbers of rings could be detected, it could in some years affect more than 13 % of the trees. In the Twin core study, 4.2 % of trees were on average annually affected by an increase or decrease of the mismatch in the number of rings. This increased significantly over the past 15 years to an average of 10 %. The CP-study, which included understorey trees, showed an even larger increase affecting up to 18.7 % of trees per year, which means that the number of trees affected almost doubled in the past 30 years. Even though understorey trees were more affected, this increase could not be explained by changes in annual increment, diameter or social class. As trees all over the study site were affected, changes in broader environmental factors such as climate may be involved.

2.4.3. Measured variables

The calculated diameters, basal areas and basal area increments not match either when comparing repeated diameter measurements with tree core calculations (CP-study) or between two cores of the same tree (Twin core study), with differences in the CP-study being slightly larger than in the Twin core study. In addition, these differences increased with time, with different social classes of trees being affected in different ways. In particular the smaller diameter understorey trees (class 5) in the CP-study showed a diameter difference of up to 180.76 % of the calculated values. All those trees share extremely narrow rings reflecting very slow growth. But even though the diameter differences were larger in those trees, the effect was still small when converting those differences into basal area terms. Here, even small differences in diameters of larger trees had a comparatively large effect on basal area differences. In general, diameters of smaller trees were rather underestimated whereas larger trees (classes 1-3) were found to show either an over- or an underestimation of diameters. But this correlation between diameter differences and the **social classes** of trees was not very significant and data showed a large variation. One reason for this could be that the social classes of trees were recorded in 2014 and it is likely that over the past 52 years some trees changed from one social class into another.

In the Twin core study, calculated diameters of two cores of the same tree matched only in 4.25 % of all measurements. When discarding the measurements of the latest 10 years, the congruence was even lower. This showed that diameter and basal area as well as increment estimates based on different tree cores of the same tree can be extremely variable. But negative and positive diameter differences were again found to be well balanced around the mean of differences for all samples. It would have been interesting to compare twin cores of all diameter classes but as the main focus of this study was to compare the longest possible times series, only larger trees with a minimum diameter of 30.0 cm were cored.

2.4.4. Underlying assumption – annual nature of rings

In age and increment studies, the ability to date tree rings is the **first requirement**. But with numbers of visible rings in twin cores not matching between cores of the same tree, their

annual formation is questionable. In general, the cambial activity of a tree is induced by growth hormones, whose production depend on environmental factors. When they are produced in abundance, radial growth is initiated around the whole circumference of a tree (Speer, 2010). Environmental stressors though can lead to an insufficient production of hormones. This can result in **missing rings** in the lower parts of the stem as hormones are created in the apical meristems and transported downwards in the phloem. This is in particular a problem for diffuse-porous trees such as *B. tawa*. In ring-porous trees, in comparison, a number of vessels appear to be produced from cambial derivates of the previous year even before hormones are produced (Evert, 2006; Speer, 2010). Thus, even if growth might not sustain throughout the whole year, those narrow rings are visible and missing rings are rare. The cambial activity is also strongly influenced by environmental stresses such as insect infestation, fire or drought. Here, it can stop for some time until this stress abates. When activity is resumed within the same growing season, it can therefore form **false rings** (Pallardy, 2008). These stressors can affect growth around the whole circumference of a tree as well as only parts of it. In addition, when the cambium of a tree is damaged on one side, it can still keep growing on the other side, forming **incomplete rings**. Ogden & West (1981) reported cases where parenchyma bands formed false rings in *B. tawa* that were potentially initiated by out-of season frost damage. These false rings did not occur around the whole circumference and they were able to detect them by tracing those rings laterally in tree discs. Harvesting of emergent podocarp trees in mixed podocarp-broadleaved forest, as occurred at the study site, removes the protective cover of the forest and leaves crowns of *B. tawa* canopy trees exposed to out-of season frosts (McKelvey, 1954) that were reported to damage them readily (Hinds & Reid, 1957). Older trees on ridges as well as recently exposed trees also showed this form of temporary dieback (M. C. Smale et al., 1986) that could influence the number of visible rings in cores. However, in increment cores it is not possible to trace rings laterally and false rings produced after frost can be extremely difficult to detect (Kelly, 1987).

These incomplete, missing and false rings as well as the general irregular cambial activity were evident in the Twin core study, where individual growth patterns showed that the numbers of rings do not match. Another stress factor that was found in both studies to be

commonly affecting the cambial activity is overstorey competition, where trees either didn't grow at all within a decade or rings were too narrow to be detected.

2.4.5. Underlying assumption – ring width

The widths of consecutive rings of *B. tawa* could be extremely variable and a significant correlation was found between those ring width differences and the mean annual increment of trees, where differences increased with radial increment. In particular in faster growing trees, a pattern of wide rings alternating systematically with narrow rings was found to be a common feature. This observation of **biennial fluctuations** of ring widths is in line with findings from Ogden & West (1981) and Dunwiddie (1979). Lloyd (1963) as well as J. Stewart (1905) and Francis (1928) suggest that trees can show more than one flush of growth in one year which leads to the formation of several rings within one year. In particular Lloyd (1963) suggests that in some species a thin band of summer wood close inside a thick band of summer wood might indicate a false ring, whereas a thin band outside a thick band indicates a separate ring. This observation could not be confirmed in this study, where biennial fluctuations showed no correlation to the number of false rings.

Differences in the width of rings are regularly used for cross-dating, where similar ring-width patterns of different trees are matched and compared against a master chronosequence (Fritts, 1976). Matching patterns can indicate responses to growth limiting environmental factors that are shared by several trees within the forest. But the **mean sensitivity analysis** for *B. tawa* returned values > 0.4 for 95.2 % of all tree cores indicating a very large variability of tree ring widths within samples. In practice, tree ring series with mean sensitivities greater than 0.4 are often considered too sensitive, as absent or micro rings may occur frequently, making tree ring dating extremely difficult (Speer, 2010).

Substantial changes in the light regime were found to induce faster growth and with that wider rings within several trees. Here, the mean and the variance of annual growth changed abruptly. When **growth releases** are induced by catastrophic events, they are commonly shared by many trees and can be used for cross-dating. In this study, harvesting induced growth releases that were used to date tree rings and detect false and missing rings.

But aside from the harvesting event, ring width characteristics rarely matched between trees and releases were most likely initiated by small scale changes affecting only very limited numbers of trees. Thus, it was impossible to date rings or detect false or missing rings within those tree cores or for those times. Under these conditions cross-dating can also become impossible.

The **second requirement** for age and increment studies based on tree cores states that the distance between two rings reflects the actual growth within that year. But large proportions of the diameter differences in the CP-study (39.8 %) as well as the Twin core study (56.2 %) were assigned to variations in tree ring width, showing that this requirement is violated.

It is generally known that the ring width is often not continuous around the circumference of the stem but can vary on different sides of the tree thus producing a ring of an irregular width (Grabner & Wimmer, 2006; Pallardy, 2008). Mechanical stresses are also known to influence the ring width and cellular structure of trees, forming tension wood that is often leading to **eccentric cambial growth** (K. T. Smith, 2008). Another observed factor for the irregular width of rings in different cores of the same tree was wedging where rings became invisible due to pinching. In increment cores this could be mainly observed close to the pith where larger percentages of the circumference of trees are visible. But it can be expected that wedging also occurs further away from the pith.

These findings were supported by the **Gleichläufigkeit** analysis, where even cores of the same tree did not show the same growth patterns. The concept of Gleichläufigkeit was often criticised for discarding important information resulting in high scores for not matching growths patterns (Baillie, 1995; Schweingruber, 1988). But in the context of this study, Gleichläufigkeit was used to examine how well increment cores reflect the actual growth of B. tawa trees by comparing two cores of the same tree. The large spread in the Gleichläufigkeit scores for the different twin core pairs ranged from 0.36 to 0.92 and increases the problem with *B. tawa* cores even further. But low Gleichläufigkeit scores did not necessarily mean that trees do not match. Rather, it showed that observed growth

patterns in one increment core of *B. tawa* were not representative of the overall growth of that tree and using them in dendrochronological studies appears questionable. False and missing rings were identified as major contributors for low scores and accounting for them increased the Gleichläufigkeit significantly by 0.21 to 0.76. But still 24 % of the difference remained unexplained by false and missing rings and were assigned to irregular cambial activity causing different increment estimates for individual cores.

2.4.6. Interaction between measured variables, counted variables and social class

In silviculture, the **periodic increment** of basal area is an important variable for the derivation of the annual yield as a basis for sustainable forest management. But with a mean basal area difference of 27.49 % in 52 years, increment cores of *B. tawa* seem to hold limited information content. A major source of the problem was found to be the number of false and missing rings. Even when the total number of rings within a period matched, the calculated increments could still differ when the period contained equal numbers of false and missing rings. While false rings were causing an underestimation, missing rings caused an overestimation. This corresponds with an overestimation (false rings) or underestimation (missing rings) of age. Differences in numbers of rings between twin cores on the other hand could not be directly related to an over- or underestimation of rings as the true age of those trees was not known. Hence they could reflect either missing rings in one core or false rings in the other core.

The **annual increment** as well as the **social classes** of trees proved to be closely related to **missing and false rings** and showed significant correlations. While missing rings were correlated with extremely slow growth (suppressed understorey trees, class 5), false rings occurred mainly in specimen growing faster than average (codominant and subdominant trees, classes 2 and 3).

Beilschmiedia tawa is extremely shade-tolerant with very low mortality rates of dominated seedlings (1 % yr^{-1} over a 22-year period) which can persist in the understorey for up to 100 years (M. C. Smale & Kimberley, 1986). The high number of possible missing rings in dominated understorey trees (class 5) has therefore to be considered when analysing cores

of those trees. It is even doubtful that sampling tree discs instead of increment cores can solve this problem. An underestimation of age and an overestimation of radial increment seem to be very difficult to avoid. This is not only the case for understorey trees but even for class 1 trees. One predominant tree with a dbh of 57.5 cm showed 359 rings at a coring height of 20 cm above ground. For the first 101 rings it was growing as an understorey tree with a mean increment of 0.8 mm yr^{-1} until growth was released at a diameter of 8.03 cm. Due to their extreme shade tolerance, *B. tawa* trees of all classes can have gone through phases of understorey growth until growth conditions changed in their favour followed by a release. Therefore not only the current social classes of trees should be taken into account when working with increment cores, as trees can have moved between classes over time.

2.4.7. Final modelling

The problems around the annual formation of rings as well as the representativeness of their widths create a large uncertainty in age and increment studies. But modelling revealed that the positive and negative differences were well balanced. As random effects can't be used for predictions, only the significant fixed effects annual increment and time were included in the **final model** that explained 99.88 % of the variation. This means that even though individual tree cores do not represent the increment of individual trees well, the sums of calculated basal areas as well as basal area increments represent the values for *B. tawa* on a stand level.

2.5. Conclusion

Parenchymatous bands in transverse sections of *B. tawa* were found to generally reflect annual rings but estimates of age, diameter, basal area and annual basal area increment of individual trees based on increment cores contain many uncertainties that are difficult to account for. Understanding the contributing factors can help evaluating their magnitude on an individual tree basis.

False and missing rings were found to be common features producing considerable errors. Trees of different social classes were affected by false and missing rings in different ways, with the main driver being the mean annual increment. During phases of faster growth, trees were found to produce additional 'false' rings that lead to an overestimation of age. In contrast, slow growing trees produced no identifiable growth rings in some years ('missing' rings), leading to underestimates of age.

Cross-dating based on the comparison of ring patterns can generally reduce this problem but high **mean sensitivities** indicated that *B. tawa* ring width is extremely variable. In addition, the analysis of twin cores from the same tree showed that the numbers of rings visible in increment cores as well as growth patterns differ even within trees. But c**hangepoint analysis** proved to be effective in accounting for those false or missing rings when the dates of catastrophic events that affected whole forest stands are known (e.g., harvesting). However, under natural conditions at Pureora it is very doubtful that individual *B. tawa* tree ring data based on increment cores can be used for dendrochronological studies.

In increment studies, the annual growth of trees is often derived from relative distances between two rings, and false and missing rings influence those results significantly. In addition, eccentricity and wedging of rings caused differences in tree ring widths. As often no repeated diameter measurements exist for native forests and the error in tree age analysis is therefore unknown, twin cores were found to be useful indicators for false and missing rings. In particular two tree cores that are taken in a horizontal angle of 90° to each other proved to be very promising. However, averaging age and increment estimates of twin

cores, which is often recommended, did not prevent the uncertainties. Twin cores should rather be used to investigate the uncertainties associated with tree core analysis and were found to be adequate to capture ring width characteristics. The closer growth patterns for those two cores match, the less likely is it that the underlying assumptions around tree core analysis are violated.

This is the case for increment studies as well as age studies. But still, this does not help with rings that are missing around the whole circumference of understorey trees where age estimates were found to be no more than an indication of a minimum age. This subsequently also affects the results of increment analysis and growths estimates should not be based on annual increment. Instead they are best based on periodic basal area increments over several years. On a stand level and including trees of all social classes, the effect of the basal area increment estimation error for understorey trees was found to be negligible.

Even though growth features of *B. tawa* seem to violate all assumptions for dependable age and increment analysis based on tree cores and results of increment studies carry all the described errors and uncertainties on an individual tree level, modelling showed that positive and negative measurement errors are well balanced, making basal area and increment calculations on a stand level reasonably reliable. This has an important impact on growth studies that are investigating basal area increments. In sustainable forest management, for example, knowledge about periodic basal area increments is paramount to determine sustainable cuts. Another application is the investigation of basal area recovery over time after disturbances. For any native tree species that is the focus of harvesting operations, the suitability of tree cores for age and increment studies of such species should be investigated in a way similar to the one demonstrated in this study.

Chapter 3

Podocarp-broadleaved forest in the central North Island, New Zealand – a forest in transition

3.1. Introduction

Forests ecosystems are constantly changing as a result of frequent and infrequent disturbances of various intensities in combination with inter- and intraspecific competition (Allen & Norton, 2000). In particular, the magnitude of disturbances has an important influence on forest composition and structure (Attiwill, 1994). But also the timing of such disturbances in regards to season and periodicity of seedfall (mast years) influence regeneration success (Beveridge, 1964). Large scale disturbances can initiate primary or alter ongoing succession (Duncan, 1991; P. Wardle, 1980; D. C. West, Shugart, & Botkin, 1981). Mixed podocarp-broadleaved forests in New Zealand were long assumed to reflect a transitional forest type from podocarp forest to broadleaved forest (McKelvey, 1952, 1963; Robbins, 1962). This succession model proposes a general trend after a cataclysmic disturbance such as volcanism from colonising scrub species via dense podocarp forests to mixed podocarp-broadleaved forest followed by broadleaved forest with only a minor component of podocarps. But the general linearity of this podocarp succession has been disputed by several other authors (Cameron, 1954; Ogden & G. H. Stewart, 1995) who suggest a rather cyclic regeneration.

Succession depends to a large degree on available seed sources and dispersal mechanisms, as well as topography, climatic factors and soil conditions. Podocarps rely to a large degree on active dispersal of seeds by fruit-eating birds such as kereru (*Hemiphaga novaeseelandiae*), tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*) (Beveridge, 1964). Different sites will have different successional pathways involving different species and time frames (B. D. Clarkson, 1990; B. D. Clarkson, B. R. Clarkson, & McGlone, 1986). In particular, accounting for the influence of soil is leading to a more differentiated view. In the Central North Island, dense podocarp stands are predominantly found on soils containing a thick layer of pumice (Norton, Herbert, & Beveridge, 1988). Similar observations of dense stands of podocarps were made on alluvial surfaces and glacial terraces in Westland (H. M. Rogers, 1999; G. H. Stewart, J. C. White, & Duncan, 1998), where poorly drained soils carry dense stands of podocarps, in particular *Dacrydium cupressinum* and *Dacrycarpus dacrydioides*. Even though these species do not favour those soils, they can

tolerate a degree of poor soil drainage which gives them an advantage over more demanding species at those sites. There is no indication that these dense stands will be replaced by mixed podocarp-broadleaved forests with increasing dominance of angiosperms, rather mixed podocarp-broadleaved forests are more typically found in sites with better drained soils (Norton & Leathwick, 1990).

3.1.1. Focus of this study

The question remains whether mixed podocarp-broadleaved forests in the Central North Island are a transitional stage between podocarp and broadleaved forest or indeed reflect a forest type that is self-perpetuating. This chapter investigates if there is any evidence that today's podocarp-broadleaved forest will evolve into a broadleaved forest over time. It will focus on an example of mixed old-growth forest on the Volcanic Plateau in the north of Pureora Forest in the Central North Island. To understand the distribution of trees as well as the spatial patterns and the processes within the forest, it is important to recognize its origin and evolution (McGlone, 1985). For this reason, the first part of this chapter is a short excursion into the history of the podocarp-broadleaved forests in the Central North Island of New Zealand. The second part elaborates the horizontal, vertical and temporal forest structures at the study site and searches for indicators of compositional or structural changes. And finally this chapter concludes with an attempt to foresee the future development of this forest.

While the first part is a review of literature, the second part is based on field data that were collected from 2011-2014. It addresses the following set of 5 general questions in order to understand the growth dynamics in mixed podocarp-broadleaved forest at the study site:

1. **What are the compositional and structural patterns of the forest?**

   This question investigates the forest composition, tree species frequencies and densities as well as the vertical structure, social structure and age structure of the forest.

2. **What are the regeneration patterns in the forest?**

   A regeneration analysis investigates the regeneration potential of selected canopy species as a predictor for future forest development.

3. **What are the growth patterns in the forest and what are their drivers?**

   Past height and diameter growth as well as temporal changes are investigated for all major canopy species. Of particular interest is whether regeneration and advanced growth of canopy tree species is determined by localised factors or if they share large-scale patterns that can be related to historic disturbance events.

4. **What are the mortality rates of the different species of emergent podocarps?**

   This question identifies changes in the composition and structure of emergent podocarps.

5. **Is it possible to predict the future of podocarps in the forest?**

   Based on the current composition, structure, regeneration, growth dynamics and mortality, a prediction for the presence and dominance of podocarps in the future forest is attempted.

3.1.2. Central North Island forest development after the last glaciation

During the maximum of New Zealand`s last glaciation (23,000-12,000 BC), forests were mainly restricted to scattered patches in a matrix of grassland and of shrubland communities. This period had probably the most influence on New Zealand`s current forest distribution (McGlone, 1985). At the end of this glaciation, temperatures began to increase and forest spread fast throughout the North Island. Here, lowland sites as well as north-facing slopes provided favourable microclimates for the establishment of trees. They were warm and sheltered but with sufficient rainfall and free from severe frost. As forests developed in the post-glacial throughout New Zealand roughly around the same time, it is likely that most present-day lowland tree species must have survived the glaciation in their current distribution range (McGlone, 1983a) at sites most sheltered from constant strong

winds, episodic drought and freezing air masses from the southern polar region (McGlone, 1985). Valley bottoms and alluvial terraces were the last sites to become forested as they kept the cool and dry climate for much longer (McGlone, 1983a).

The first forests that established in the northern and central North Island in the post-glacial period were podocarp-angiosperm communities that were dominated by *Prumnopitys taxifolia* for around 4,000 years (Harris, 1963; McGlone & Topping, 1977). With the climate becoming wetter and cooler again at around 8,000 BC, *D. cupressinum* became more dominant. It was well adapted to the changing conditions, showing an almost pandemic distribution (McGlone, 1983a). But the forest structure and composition was never stable during this mid post-glacial period. The proportion of many forest taxa was constantly changing with the climate regularly alternating and the soils maturing (McGlone & Topping, 1977).

3.1.3. The Taupo-eruption and its influence on forest development

Besides changes in climate, volcanic activity in form of large cataclysmic eruptions shaped the geology and the forests in particular in the Central North Island of New Zealand (B. R. Clarkson, B. D. Clarkson, & Patel, 1992; B. R. Clarkson, Patel, & B. D. Clarkson, 1988; Healy, 1982; McGlone & Topping, 1977; C. J. N. Wilson, 1993).The largest rhyolitic eruption within the past 7,000 years was the Taupo Eruption (Baumgart, 1954; Baumgart & Healy, 1953; C. J. N. Wilson, 1985) that occurred c. AD 232 (Hogg, Lowe, Palmer, Boswijk, & Ramsey, 2011). An inferred volume of 65 km^3 eruption products (equivalent to 19 km^3 magma and 3 km^3 lithic debris), 20 km^3 ignimbrite deposits and 20-60 km^3 of primary eruptive material damaged and destroyed 20,000 km^2 of forest. More than 30,000 km^2 of land were covered by airfall deposits more than 10 cm thick (C. J. N. Wilson & G. P. L. Walker, 1985) up to a distance of 170 km east of the vent. The individual level of forest destruction was highly variable and depended on the distance from the eruptive centre as well as the local topography.

While areas closer to the eruption centre were completely destroyed and buried under ash and debris, others that were further away were only damaged to varying degrees. Acid rain, hot ash and toxic chemicals leaching from it will have defoliated large areas but younger

trees and more robust species will have survived the eruption (Wilmshurst & McGlone, 1996).

The pre-Taupo eruption forests were described by McGlone & Topping (1983), B.R. Clarkson et al. (1992, 1995, 1988) and Wilmshurst & McGlone (1996) based on plant macrofossils such as leaves, seeds and wood as well as pollen and charcoal remains in lake and peat sediment cores. In general, podocarp-broadleaved forest covered most of the Central North Island with podocarps such as *D. cupressinum* and *P. taxifolia* being generally dominant. Under these, a dense layer of various angiosperm tree species was found. After the eruption, trees revegetated the central North Island in probably less than 250 years. Centres of this revegetation were the damaged forests that survived the aftermath of the volcanic eruption, soon forming forests with similar species composition to those that were present before the eruption (J. L. Nicholls, 1963). But in some areas, the composition of pre-eruption forest different considerably from the post-eruption forest (B. R. Clarkson et al., 1995). An important role for forest recovery and species dominance played here the local climate (Wilmshurst & McGlone, 1996), with wetter sites supporting faster growth.

Wherever the vegetation was completely destroyed, pioneer plants such as *Pteridium esculentum* or *Leptospermum scoparium* acted as typical colonizers of bare pumice land, followed by different species of the genera *Pittosporum* and *Pseudopanax* together with *Weinmannia racemosa*. These scrublands with their attractive fruits then attracted abundant birdlife such as kereru, tui, bellbird and silvereye (*Zosterops lateralis*) carrying seeds of light-demanding podocarp species from forest remnants over large distances (Beveridge, 1964). Dense mixed podocarp forest subsequently developed with stockings of more than 100 trees ha^{-1} with dbh > 30cm and *P. taxifolia* and *D. cupressinum* being dominant, as well as *Podocarpus totara* and *Prumnopitys ferruginea*. Early pioneer species such as *W. racemosa* will at this stage have been the most abundant angiosperm. With podocarps growing taller and competition reducing stockings to 40 trees ha^{-1}, other shrub angiosperms established and taller angiosperms such as *Elaeocarpus dentatus* started to establish. Later, shade-tolerant angiosperms such as *Beilschmiedia tawa* became abundant, forming a second canopy under tall podocarps of stockings of around 25 trees ha^{-1}. The angiosperm pioneers

like *W. racemosa* were at this stage becoming less abundant. These podocarp-broadleaved forests are believed to lose their podocarp component, in particular light-demanding *P. totara* and *P. taxifolia*, with podocarp stockings dropping to 20 trees ha^{-1} and angiosperms like *Metrosideros robusta* becoming more frequent. *B. tawa* then became the most dominant tree species (45 trees ha^{-1}) and the only podocarp species remaining in noticeable numbers were supposed to be shade-resistant *D. cupressinum* and shade-tolerant *P. ferruginea* with stockings of less than 10 trees ha^{-1} (McKelvey, 1952, 1963). Over time those podocarps were believed to completely disappear due to competition from shade-tolerant angiosperms (Cockayne, 1928b).

Occurrence and dominance of the different tree species, however, were strongly influenced by the new soils that were derived from volcanic ash showers and ground-flow deposits of various thicknesses (J. L. Nicholls, 1983, 1986). While dense stands of podocarps such as *D. cupressinum*, *P. ferruginea*, *P. taxifolia*, *P. totara* and *D. dacrydioides* are found on thick layers of pumice soil, angiosperms are more abundant on weathered loams, forming forests with varying mixtures of podocarp and angiosperm tree species (Masters et al., 1957). In addition, climatic changes over the past 1800 years with shifts in precipitation patterns and temperatures have affected the successional pathways and forest patterns (Leathwick & N. D. Mitchell, 1992; McKelvey, 1952).

Whether or not the present podocarp-broadleaved forests in the Central North Island originate from dense podocarp forests or from older mixed forests, is difficult to investigate. The general thickness of the pumice layer in the Central North Island indicates that the destruction of the pre-Taupo forest has been widespread (Norton et al., 1988) but the fast re-vegetation, with species composition similar to the pre-Taupo forests indicate that a primary succession might have been initiated by scattered mixed forests that have survived as a seed source, even if heavily damaged (B. D. Clarkson, 1990; J. L. Nicholls, 1963). There are indications that these post-Taupo mixed podocarp-broadleaved forests on the Volcanic Plateau in the Central North Island may follow a successional pathway similar to McKelvey's (1963) hypothesis, where podocarps are now slowly replaced by angiosperms (M. C. Smale et al., 2016).

3.2. Methods

3.2.1. Research setup

This study was conducted in old-growth podocarp-broadleaved forest in the Pouakani Block of Pureora Forest. It included the 15 ha unharvested control block (A-Block) of the 1961 FRI selective logging trial (Figure 3) and adjacent undisturbed forest. The selective harvesting trial involved an intensive cruising that focused on merchantable podocarp trees, where all podocarps of millable size were tagged in 1959 and their diameters measured. In addition, their health status was recorded and reassessed in 1980 and 2004.

Forest composition and structure

For the structural analysis, 24 randomly selected sampling points were established in 2011 of which 11 points were located in the control block and 13 in the adjacent undisturbed forest. The main features of the structural composition of the forest were recorded with the help of 10 variables (Table 15).

Table 15. Variables recorded and calculated for the structural analysis

Recorded variables	**Description**
Tree species	Tree species list (see Appendix)
Tree height	Height measurement - Vertex 3 (unit: metre)
Tree dbh	Circumference measuring tape (unit: centimetre)
Social position of tree	Modified Kraft's classes (see Chapter 2, Table 8)
Number of tiers	Height measurement - Vertex 3 (unit: metre)
Stage of forest development	4 phases: Gap, Building, Mature and Senescent phase
Calculated variables	
Tree species frequency	Spatial distribution of tree species (presence – absence)
Tree species abundance	(unit: trees ha^{-1})
Tree age	tree ring analysis based on increment cores (unit: year)

A fixed-area method in the form of circles was used as the ratio of the edge length of a plot to the plot area is smaller for circles than for square or rectangular shapes, which reduces edge effects and therefore errors (Krebs, 1999). A preliminary study showed that the frequency of trees within the natural forest generally varies with their dimensions. To reduce

unnecessary sampling effort, a sampling design with nested concentric plots was applied as suggested by Husch et al. (2003) and Newton (2007). The chosen diameters of those plots were 3, 6, 12 and 20 m radius, respectively (Figure 38). Their diameters reflected the assumed average height of trees measured within those plots.

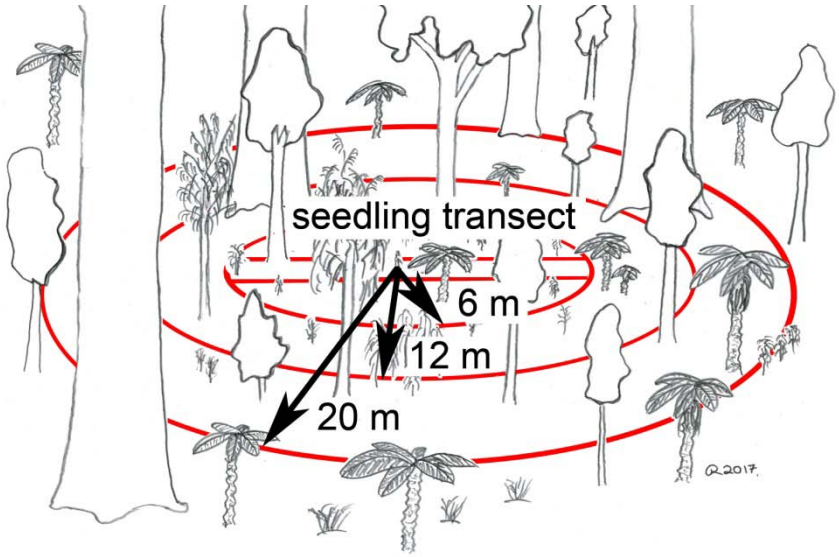

Figure 38. Sampling plot design with concentric circular plots of different sizes

Regeneration analysis

In addition to those circular plots, a seedling transect of 12 x 2 m was laid out in the centre of each plot. This transect was subdivided into 12 square plots of 1 x 2 m each and seedlings and saplings of the 8 main canopy species were recorded in different height classes (Figure 39). This approach was chosen to provide an estimate of variability in seedling distribution.

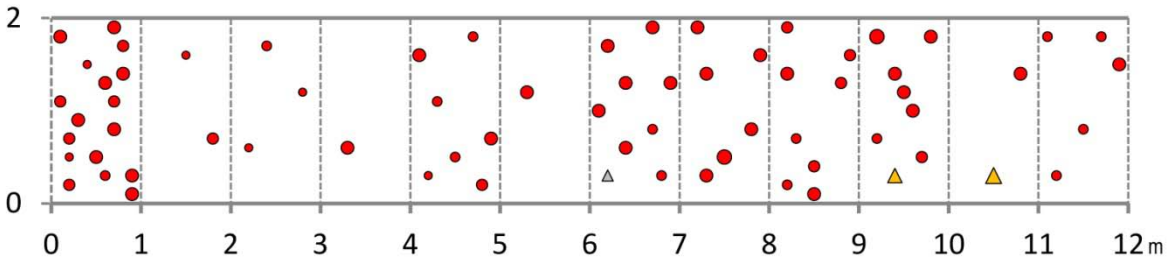

Figure 39. Regeneration transect of 12 x 2 m divided into 1 x 2 m subplots; red dots are seedlings and saplings of *Beilschmiedia tawa*, grey triangle is seedling of *Prumnopitys ferruginea* and orange triangles are saplings of *Prumnopitys taxifolia;* the larger the dot, the larger the height class

Size classes

All trees within the 20 m plot were assigned to different size classes and subclasses (Table 16). This approach follows in general the definitions of the Silviculture Working Group of the Society of American Foresters (D. L. Adams et al., 1994), where the terms do not refer to the actual age classes of trees but to their life stages defined by their size. This approach seemed appropriate as in particular young podocarps can sometimes take between 20 and 50 years to reach 1- 2 m in height (Beveridge, 1973) and the actual age of such a 'seedling' is not known until it is cut and growth rings analysed. In this study it was not desirable to destructively sample those young trees as it only focuses on the number of trees that reach the next life stage and the abundance of trees in different height classes. Seedlings were less than 140 cm tall and assigned to three height classes. Trees taller than 140 cm were assigned to dbh classes, grouped into 'saplings', 'pole trees' and 'mature trees'. This classification was developed for the main tree species in the focus of this study and it is apparent that many smaller tree species in podocarp-broadleaved forest do reach maturity much earlier than it takes them to reach the size class 'mature'.

Table 16. Tree size classes used in this study

Size classes	Tree subclass	Measurement	Tree size
Seedling	1	height	0 – 20 cm
Seedling	2	height	21 – 50 cm
Seedling	3	height	51 – 140 cm
Sapling	4	dbh	0 – 2.4 cm
Sapling	5	dbh	2.5 – 4.9 cm
Pole	1	dbh	5.0 – 9.9 cm
Pole	2	dbh	10 – 19.9 cm
Mature	1	dbh	20 – 39.9 cm
Mature	2	dbh	40+ cm

Social status of trees

Height and diameter are absolute values, useful for describing individual trees dimensions. But these variables do not specify the competition status of a tree within its environment. This is of particular importance when the canopy of a forest is not continuous but shaped by small-scale disturbances in the upper tiers through windfall or death of individual overstorey trees. Therefore, each sampled tree within a plot was assigned to one of 5 social classes as described in Chapter 2 to account for inter- and intraspecific competition.

Sampling plot setup

For the different plots, different sampling criteria were applied in accordance with the different life stages and size classes of the tree species in focus (Table 17). In the belted transect, seedlings (subclass 1-3) and saplings (subclass 4-5) of *D. dacrydioides*, *D. cupressinum*, *P. trichomanoides*, *P. totara*, *P. ferruginea*, *P. taxifolia* and *B. tawa* were recorded.

Table 17. Sizes of different plots and measurements taken

Plot name	Dimension	Size	Measurements
Belted transect	12 x 2 m	24 m²	7 main canopy species; belted transect that is subdivided into 12 rectangular plots of 1 x 2 m; seedlings are counted and attributed to the 3 different subclasses; saplings are counted and attributed to the 2 different subclasses
Sapling Plot (circular)	3 m radius	28.3 m²	All species; saplings and pole trees of subclass 1; dbh measurements as well as polar coordinates within the plot taken
Pole Plot 1 (circular)	6 m radius	113.1 m²	All species; pole trees of subclass 2; dbh measurements as well as polar coordinates within the plot taken
Pole Plot 2 (circular)	12 m radius	452.4 m²	All species; pole trees of subclass 2; dbh measurements as well as polar coordinates within the plot taken
Pole Plot 3 (circular)	12 m radius	452.4 m²	All species; all pole trees of social class 1-3; dbh measurements as well as polar coordinates within the plot taken
Mature Plot 1 (circular)	12 m radius	452.4 m²	All species; mature trees of subclass 1; dbh measurements as well as polar coordinates within the plot taken
Mature Plot 2 (circular)	20 m radius	1,256.6 m²	All species; mature trees of subclass 2; dbh measurements as well as polar coordinates within the plot taken

In all but one of those plots, the tree diameter determined whether or not an individual was to be sampled. Sampling criterion for Pole Plot 3 was based on the social classes of trees (classes 1-3) to investigate what tree species dominated the pole size classes. This was used as a measure to investigate potential competition below the main canopy, as the canopy is recruited from the pole classes.

Vertical structure

To get an indication of the vertical structure of the forest, the heights of 510 trees in different life stages were measured in every 20 m plot. In this way, different canopy tiers could be identified and distinguished. In addition, height measurements of trees of the

different life stages assisted in the investigation of height/dbh and height/age relationships. In particular the latter relationship is an indicator for longitudinal growth rates. These values reflect growth conditions and are assumed to vary within the lifespan of a tree.

Age estimation

Another measure of the structure of a forest is the age distribution of its trees. Podocarps of small and medium diameters (10-50 cm dbh) were found to be too rare in the forest for reliable age and growth modelling. Therefore, another 8 non-random sampling points were established at sites where podocarps of those dimensions occurred in addition to the 24 randomly selected sampling points. The sampling design at those non-random sampling points was equivalent to the design at the randomly selected sampling points. To non-destructively sample the age of the species in focus of this study, increment cores were taken from 204 randomly selected trees of all size classes in each plot at ground level (0.3 m) (Table 18). These cores were analysed using the approach described in Chapter 2.

Table 18. Tree species that were cored and numbers of cores taken

Dacrycarpus dacrydioides		3
Dacrydium cupressinum		18
Phyllocladus trichomanoides		2
Prumnopitys ferruginea		45
Beilschmiedia tawa		101
Elaeocarpus dentatus		35
	total	**204**

As trees get older, they are known to lose their decay resistance through fungitoxic heartwood extractives being polymerized into non-toxic extractives (Packman, 1960; Rudman, 1965). This limits a tree's ability to prevent fungal infections caused for example by external wounds and can cause internal decay (Lindenmayer, Cunningham, Donnelly, Tanton, & Nix, 1993). This decay was found to be positively correlated with tree diameter (Harper, Mccarthy, & van der Ree, 2005). As for tree age estimation based on tree cores, undamaged timber is a prerequisite, all trees selected for coring were tested for internal decay using the field method described by Boyce (1961). Here, a rubber mallet is used to create stress waves in the timber of a tree by striking its trunk. The sonic differences in the audible sounds of a healthy tree and a tree with internal decay were used to evaluate the

decay of a tree and select trees > 50 cm diameter for coring (Mucciardi, Luley, & Gormally, 2011). When sounding did not return a clear result, a tree was not cored. This was used as safety measure, as it could not be ruled out that those trees were still infected. Increment coring can spread fungi into healthy wood by opening compartmentalised decay, which was found to potentially accelerate internal decay and finally tree death (Norton, 1998).

Growth patterns and disturbance history

In many species, annual changes of narrow and wide rings are often accompanied by general phases of slow and fast growth (Schweingruber, 1993). Here, abrupt changes in the light environment can induce such a rapid growth response of individual trees, in particular in light-demanding tree species. But podocarps such as *D. cupressinum* and *P. ferruginea* are shade-resistant and shade-tolerant respectively (Lusk et al., 2009, 2015) with bilaterally compressed short leaves being well adapted to low light conditions (Brodribb & Hill, 1997). They were reported to be able to grow constantly but slowly for decades until they finally reach the canopy (Bond, 1989; Ebbett & Ogden, 1998; Enright, Bartlett, & De Freitas, 1993). However, Lusk & Smith (1998) found that gap-forming disturbances can release growth in those species and subsequently promote advanced regeneration into the main canopy. To investigate, whether the canopy tree species at the study site share a large scale disturbance history or if individual growth is independent and spatially restricted, the annual increment was calculated for all cored trees and a changepoint analysis that is detecting changes in the mean and variance of radial increment was used to identify historical growth release and suppression events in all cored trees following the procedures and methods elaborated in detail in Chapter 2.

Mortality

When the selective logging trials were set up in 1959, all emergent podocarps of merchantable size in those blocks were tagged and measured. In 2002, these trees were retagged and remeasured. The diameters in 1959 and the number of remaining trees in 2002 were used for a simplified modelling approach of the mortality of emergent podocarps in diameters classes from 60 cm to 200 cm. With only two recordings in time, the linear model is only expected to be indicative for a mortality trend.

Growth cycle

The crown structure and diameter distribution of a forest can be used to examine its regeneration dynamics. While even-aged forests with a continuous canopy often originate from large-scale disturbances (Ogden, 1988; J. A. Wardle, 1984), uneven canopies with gaps reflect rather small-scale disturbances (Duncan, 1991; Lusk & B. Smith, 1998).

To investigate the canopy pattern as a reflection of the scale of past disturbances at the study site, four general phases of forest growth: gap phase, building phase, mature phase and senescent (degenerate) phase (Watt, 1947), were assigned to each 40 m diameter circular sampling plot on the basis of the approach proposed by Veblen (1992). The gap phase was defined as the earliest life stage, where canopy disturbances enhance the establishment and growth of regeneration until saplings form a canopy. The building phase was defined as the time it takes regenerating canopy tree species to reach the main canopy. In the mature phase, trees are growing within the main canopy while height growth slows down significantly for most angiosperm species but continues for the podocarps. Once they passed this canopy, there is no more angiosperm competition for light. The time it takes for trees to reach the senescent phase in the forest depends on the individual species. At that stage, canopy trees start to lose their vitality and internal decay develops. The crowns show distinct gaps and dead branches that are not replaced any more.

To allow for a high heterogeneity, a maximum number of 4 phases could be assigned to each plot. This part of the study focused on the forest canopy structure and disturbance history but not on the exact size of the area of each growth phase. Therefore, only the number of growth phases occurring within each plot was recorded instead of their size. To establish time frames for each growth phase, increment cores were taken from each phase within each plot. In addition, aerial photos from 1950, 1963, 1984 and 2010 were used to account for stand history, disturbances and gap phase duration analysis in terms of tree fern colonisation.

Statistical analysis

All statistical modelling in this chapter was carried out using R-studio version 1.0.136 and standard statistical methods were used to analyse the frequencies and densities of trees. For comparison reasons, densities of trees, saplings and seedlings of the various plots were converted into hectare values. The vertical structure of the forest was modelled in form of height-dbh curves and height-age curves for the 10 most abundant species testing 14 non-linear 2-parameter and 3-parameter functions as described by Mehtätalo et al. (2015) with the help of the R-package lmfor version 1.1 (Mehtätalo, 2015). The relationships between age and diameter were analysed using standard linear regressions. For the diameter growth analysis, mean annual increments and mean annual periodic increments including standard error and standard deviation were calculated. For the changepoint analysis in this study, multiple changepoints were detected using changes of the mean as well as changes of the variance as described by Killick et al. (2012) and with the help of the 'Changepoint' R-package (Killick & Eckley, 2013). This method allowed accounting for overfitting by applying penalty values that depended on the individual growth patterns of the tree species. A simple linear regression was used for the mortality analysis as only two recordings in time were available.

3.3. Results

3.3.1. Forest composition

A total number of 21 tree and shrub species was found in the sampled plots (Table 19). Of those, 6 species were gymnosperms belonging to the family Podocarpaceae. Six of the angiosperm tree species were large trees while 8 belonged to the group of smaller trees. Only one species of shrub was found. In addition to the tree and shrub species, 4 tree fern species were recorded. Even though a species list prepared at the study site before sampling plots were established showed 8 gymnosperm tree species, 67 angiosperms, 2 monocotyledonous species and 4 tree fern species generally occurring at the study site (see Appendix), many of them were not present in any of the sampling plots. These species were found to be very rare and the chosen sampling methods are not designed to sample rare species.

Table 19. Tree and tree fern species found in sampling plots at the study site

Scientific name	Common name
Gymnosperms (large trees)	
Dacrycarpus dacrydioides	kahikatea
Dacrydium cupressinum	rimu
Phyllocladus trichomanoides	tanekaha
Podocarpus totara	tōtara
Prumnopitys ferruginea	miro
Prumnopitys taxifolia	matai
Angiosperms (large trees)	
Beilschmiedia tawa	tawa
Elaeocarpus dentatus	hinau
Elaeocarpus hookerianus	pokaka
Knightia excelsa	rewarewa
Nestegis cunninghamii	black maire
Nestegis lanceolata	white maire
Angiosperms (small trees)	
Carpodetus serratus	putaputaweta
Melicytus ramiflorus	mahoe
Myrsine australis	mapou
Pennantia corymbosa	kaikomako
Pittosporum eugenioides	lemonwood
Pseudopanax arboreus	fivefinger
Pseudopanax crassifolius	lancewood
Weinmannia racemosa	kamahi
Angiosperms (shrubs)	
Coprosma dumosa	
Tree ferns	
Cyathea dealbata	silver fern
Cyathea smithii	soft tree fern
Dicksonia fibrosa	ponga
Dicksonia squarrosa	wheki

3.3.2. Tree species frequency

Based on records of 1,241 trees, the species found at the study site were not evenly distributed throughout the forest but occurred in different frequencies (Table 20). *Beilschmiedia tawa* was the only species that was found at every sampling point (100 %), followed by *P. ferruginea* (83 %), *D. cupressinum* (79 %) and *E. dentatus* (67 %). All other angiosperms except for *Nestegis lanceolata*, *Melicytus ramiflorus*, *W. racemosa* and *Pseudopanax crassifolius* were rare and occurred only at 1-2 sampling points. Among the gymnosperms, *P. totara* and *Phyllocladus trichomanoides* were the rarest. The tree fern *Dicksonia squarrosa* is a common feature of the forest, occurring at 83 % of the sampling points, while *Cyathea smithii* was present at every second sampling point. The other two tree fern species *Dicksonia fibrosa* and *Cyathea dealbata* were not common.

But even though some species were found to be generally common, they were not common in all diameter classes. The only exception was *B. tawa,* the most frequent tree species in all diameter classes up to 90 cm dbh, its upper diameter limit. *Elaeocarpus dentatus* also had a continuous appearance in all diameter classes up to 60 cm dbh, with a maximum frequency around the 15-30 cm classes. Single individuals of up to 104 cm dbh were also recorded but rare. Frequencies of *N. lanceolata*, *P. crassifolius* and *W. racemosa* were clustered around the 15 cm classes and *M. ramiflorus* around the 15 to 30 cm classes.

Prumnopitys ferruginea was the only podocarp that was found in almost every diameter class even though it showed a bi-modal frequency, clustering around the 10-30 cm classes and then again in the highest diameter classes. A similar bi-modal frequency distribution occurred in *D. cupressinum*. But while *P. ferruginea* was more frequent in the lower diameter classes, *D. cupressinum* was more frequent in the highest diameter classes. *Dacrycarpus dacrydioides* and *P. taxifolia* occurred in the diameter classes > 100 cm, apart from single individuals in the 80-100 cm classes. *Podocarpus totara* appeared only in the highest diameter class >100 cm and only one single individual of *P. trichomanoides* was found in the 30 cm class.

Table 20. Frequency (%) of plots where the different species in the different diameter classes (cm) occur; the names of the classes refer to the upper limits (centimetres) of each class

Diameter classes:	10	15	20	30	40	50	60	70	80	90	100	>100	all Ø
Gymnosperms													
Dacrycarpus dacrydioides											4	21	25
Dacrydium cupressinum	13	13	8	13					13	4	17	58	79
Phyllocladus trichomanoides				4									4
Podocarpus totara												8	8
Prumnopitys ferruginea	25	50	21	17	4	4		8	17	13	8	13	83
Prumnopitys taxifolia									4			33	38
Angiosperms (large trees)													
Beilschmiedia tawa	79	92	96	88	67	63	54	38	17	17			100
Elaeocarpus dentatus	4	42	38	46	21	8	13		8			4	67
Elaeocarpus hookerianus				4									4
Knightia excelsa					4	4				4			13
Nestegis cunninghamii	4	4											4
Nestegis lanceolata	17	21	17	8				4					42
Angiosperms (small trees)													
Carpodetus serratus	4												4
Melicytus ramiflorus		21	17	21									33
Myrsine australis		4											4
Pennantia corymbosa				4									4
Pittosporum eugenioides		4		4									8
Pseudopanax arboreus		4	8										8
Pseudopanax crassifolius	4	13	8	4									17
Weinmannia racemosa	8	29	8	8									33
Angiosperms (shrubs)													
Coprosma dumosa	4												4
Tree ferns													
Cyathea dealbata													8
Cyathea smithii													46
Dicksonia fibrosa													17
Dicksonia squarrosa													83

As the podocarps occurred mostly in diameter classes > 100 cm, it is worthwhile having a closer look at them (Table 21). *Dacrydium cupressinum* is the most frequent podocarp in the highest diameter classes and appears in all classes from 80-160 cm. *Prumnopitys ferruginea* reaches its maximum in the 80-90 cm classes, with single individuals reaching up to the 130 cm class. *Dacrycarpus dacrydioides* appears in the largest diameter classes scattered

between 95 and 200 cm diameter and no trees of this species were found in random sampling plots in the 10-90 cm classes. *Prumnopitys taxifolia* showed a similar distribution, not occurring in the lower diameter classes but relatively frequent in the 110 cm class with scattered individuals from 70.5 cm to 146 cm. At the study site, *P. totara* is a very rare podocarp species that only appears with single individuals in the 160 and 180 cm classes while *P. trichomanoides* does not occur in larger diameter classes at all.

Table 21. Frequency (%) of plots where the different podocarp species in the different diameter classes (cm) occur; the names of the classes refer to the upper limits (centimetres) of each class

Diameter classes:	80	90	100	110	120	130	140	150	160	170	180	190	200
Gymnosperms													
Dacrycarpus dacrydioides			4			4					8	4	4
Dacrydium cupressinum	13	4	17	17	17	33	17	13	13		8		
Phyllocladus trichomanoides													
Podocarpus totara									4		4		
Prumnopitys ferruginea	17	13	8	8		4							
Prumnopitys taxifolia	4			21	4		4	4					

3.3.3. Tree densities

Beilschmiedia tawa was the most abundant tree species, with an overall mean density of 2,076 trees ha^{-1}. It was 11 times more abundant than *P. ferruginea* with 182 trees ha^{-1} and 13 times more abundant than *E. dentatus* with 158 trees ha^{-1}. *Nestegis lanceolata* (90 trees ha^{-1}) and *W. racemosa* (79 trees ha^{-1}) were the only other species with more than 50 trees ha^{-1}. *Dacrydium cupressinum* showed a mean density of 36.5 trees ha^{-1}, while all other podocarps were rare with densities of less than 5 trees ha^{-1}. In general, the angiosperms showed diameter distributions approaching a reverse-J shaped curve. This pattern was most evident for *B. tawa*, where numbers dropped continuously from 1259 tree ha^{-1} in the 10 cm class to 1.7 trees ha^{-1} in the 90 cm class, but also for the podocarp *P. ferruginea* (Table 22). This trend was to a lesser extent visible in the angiosperm species *N. lanceolata*, *W. racemosa*, *P. crassifolius* and *M. ramiflorus*. *Elaeocarpus dentatus* showed a slight left-modal curve where numbers peaked at 48 trees ha^{-1} in the 15 cm class. For display reasons, the density of this species of 0.3 trees ha^{-1} in the 100-109.9 cm class is missing in the table. All

other angiosperm species were either shrubs (e.g. *Coprosma dumosa*) or too rare (e.g. *Myrsine australis*, *Pittosporum eugenioides*) to see a pattern in their diameter distribution.

Having a closer look at the diameter distributions of the podocarps, *P. ferruginea* appeared in almost all diameter classes up to 130 cm, even though with very low abundance of 0.3-1.3 trees ha^{-1} in diameter classes between 30 and 130 cm. With an overall density of 4.6 trees ha^{-1}, *P. ferruginea* was the second most abundant podocarp species in diameter classes > 60 cm. *Dacrydium cupressinum* showed abundances of 3-6 trees ha^{-1} in the diameter classes up to 30 cm, while it was missing in the classes 30-70 cm. It then appeared again in classes 70-170 cm with densities of 0.7-2.7 trees ha^{-1} and a peak in the 120-129.9 cm class. However, it was the most abundant podocarp species in diameter classes > 70 cm with an overall density of 14.3 trees ha^{-1}. *Prumnopitys taxifolia* was absent in all diameter classes up to 70 cm, at which time it started to appear in classes up to 150 cm with low abundances of 0.3-1.7 trees ha^{-1}, showing a peak in the 100-109.9 cm class. Here it appeared almost as often as *P. ferruginea* with an overall density of 3.3 trees ha^{-1} in diameter classes > 70 cm. *Dacrycarpus dacrydioides* did not appear at all in any of the diameter classes up to 90 cm and only extremely low densities of 0.3-0.7 trees ha^{-1} were found in the larger diameter classes up to 200 cm. The overall density in diameter classes > 70 cm was accordingly low with only 2.0 trees ha^{-1}. *Podocarpus totara* and *P. trichomanoides* were the rarest of the podocarp species. *Podocarpus totara* was completely absent in all diameter classes below 150 cm with only 2 trees being measured with 150.5 and 178.7 cm diameter accounting for an overall density of 0.7 trees ha^{-1}. *Phyllocladus trichomanoides* on the other hand appeared with a density of 1 tree ha^{-1} in the 25-29.9 cm class.

Table 22. Mean densities (individuals ha^{-1}) ± one standard error of the different tree species in different diameter classes (cm)

Gymnosperms	< 10 cm	10-14.9	15-19.9	20-24.9	25-29.9	30-39.9	40-49.9	50-59.9	60-69.9	70-79.9	80-89.9
Dacrycarpus dacrydioides											
Dacrydium cupressinum	5 ± 3	4 ± 2	6 ± 4	3 ± 3	4 ± 2					1 ± 0.5	0.7 ± 0.7
Phyllocladus trichomanoides					1 ± 1						
Podocarpus totara											
Prumnopitys ferruginea	93 ± 53	46 ± 12	25 ± 15	8 ± 6	4 ± 3	1 ± 1	0.3 ± 0.3		0.7 ± 0.5	1.3 ± 0.6	1 ± 0.5
Prumnopitys taxifolia										0.3 ± 0.3	0.3 ± 0.3
Angiosperms (large trees)											
Beilschmiedia tawa	1,259 ± 227	391 ± 59	235 ± 37	88 ± 12	32 ± 8	40 ± 7	16 ± 3	7 ± 1	4 ± 1	2 ± 1	1.7 ± 0.8
Elaeocarpus dentatus	29 ± 29	48 ± 16	38 ± 13	19 ± 6	14 ± 4	7 ± 3	1 ± 1	1 ± 0.5		0.7 ± 0.5	
Elaeocarpus hookerianus					1 ± 1						
Knightia excelsa						1 ± 1	0.3 ± 0.3				0.3 ± 0.3
Nestegis cunninghamii	15 ± 15	4 ± 4									
Nestegis lanceolata	60 ± 35	17 ± 9	11 ± 6	1 ± 1	1 ± 1				0.3 ± 0.3		
Angiosperms (small trees)											
Carpodetus serratus	29 ± 29										
Melicytus ramiflorus		24 ± 12	9 ± 5	4 ± 2	2 ± 1						
Myrsine australis		4 ± 4									
Pennantia corymbosa				1 ± 1							
Pittosporum eugenioides		4 ± 4			1 ± 1						
Pseudopanax arboreus		1 ± 1	6 ± 5								
Pseudopanax crassifolius	15 ± 15	12 ± 7	5 ± 4	1 ± 1							
Weinmannia racemosa	45 ± 44	25 ± 9	5 ± 4	4 ± 3							
Angiosperms (shrubs)											
Coprosma dumosa	29 ± 29										

Gymnosperms	90-99.9	100-109.9	110-119.9	120-129.9	130-139.9	140-149.9	150-159.9	160-169.9	170-179.9	180-189.9	> 190 cm
Dacrycarpus dacrydioides	0.3 ± 0.3			0.3 ± 0.3					0.7 ± 0.5	0.3 ± 0.3	0.3 ± 0.3
Dacrydium cupressinum	1.7 ± 0.8	1.7 ± 0.8	1.3 ± 0.6	2.7 ± 0.8	2.0 ± 1.0	1.0 ± 0.5	1.7 ± 1.1		0.7 ± 0.5		
Phyllocladus trichomanoides											
Podocarpus totara							0.3 ± 0.3		0.3 ± 0.3		
Prumnopitys ferruginea	0.7 ± 0.5	0.7 ± 0.5		0.3 ± 0.3							
Prumnopitys taxifolia		1.7 ± 0.7	0.3 ± 0.3		0.3 ± 0.3	0.3 ± 0.3					

Densities of tree ferns varied considerably throughout the forest (Table 23). The most abundant species was *D. squarrosa* with a mean density of 437 stems ha^{-1}. They appeared as single individuals as well as in clusters of small or large groups. *Cyathea smithii* was another common tree fern species that was found in small groups or as individuals. *Cyathea dealbata* and *D. fibrosa* were rare species in the forest and only single individuals were found infrequently.

Table 23. Mean density (individuals ha^{-1}) ± one standard of 4 tree fern species at the study site

Tree ferns	density	min - max	SD
Cyathea dealbata	3 ± 2	0 – 44	10
Cyathea smithii	140 ± 44	0 – 818	217
Dicksonia fibrosa	12 ± 7	0 – 133	34
Dicksonia squarrosa	437 ± 158	0 – 3204	773

3.3.4. Regeneration

Seedlings and saplings were recorded and measured in 24 belted transects with a total of 576 m². The frequencies of the 7 sampled species varied considerably between species (Table 24). In general, frequencies decreased with increasing tree size. *Beilschmiedia tawa* was the most frequent tree species in all seedling and sapling classes. In the smaller seedling classes 1 and 2 it was found in almost every plot. Even in the higher classes 3 and 4 it was still found in around 80 % of the plots. *Prumnopitys ferruginea*, *D. dacrydioides* and *D. cupressinum* were among the most frequent podocarp species followed by *P. taxifolia*. No seedlings or saplings of *P. trichomanoides* or *P. totara* were found in any transect. A comparison between the frequencies of the different species shows the order:

B. tawa (50 %) > *P. ferruginea* (24 %) > *D. dacrydioides* (10 %) > *D. cupressinum* (9 %) > *P. taxifolia* (6 %)

Table 24. Frequency (%) of plots in which seedlings and saplings of the different height classes occurred (*n* = 24)

Gymnosperms	**1**	**2**	**3**	**4**	**5**
Dacrycarpus dacrydioides	54	21	4	-	-
Dacrydium cupressinum	38	17	13	4	4
Phyllocladus trichomanoides	-	-	-	-	-
Podocarpus totara	-	-	-	-	-
Prumnopitys ferruginea	83	29	46	25	13
Prumnopitys taxifolia	17	8	13	8	-
Angiosperms					
Beilschmiedia tawa	100	92	83	79	50

Similar results are evident when comparing the densities of seedlings and saplings of the different tree species (Table 25). *Beilschmiedia tawa* with a total of 13,838 individuals ha^{-1} was by far the most abundant species in all size classes, followed by *P. ferruginea* with 3,645 individuals and *D. dacrydioides* with 1,875 individuals. *Dacrydium cupressinum* was reasonably rare with less than 1,000 individuals ha^{-1} followed by *P. taxifolia* with only 260 sampled individuals. All species showed the highest abundance in the smallest size class and numbers deceased with an increase in size. The overall abundance of the different species can be expressed as:

B. tawa (68 %) > *P. ferruginea* (18 %) > *D. dacrydioides* (9 %) > *D. cupressinum* (4 %) > *P. taxifolia* (1 %)

Table 25. mean densities (individuals ha^{-1}) ± one standard error of seedlings (class 1-3) and saplings (class 4-5)

Gymnosperms	**1**	**2**	**3**	**4**	**5**	**Total**
Dacrycarpus dacrydioides	1,719 ± 591	139 ± 74	17 ± 17	-	-	1,875
Dacrydium cupressinum	434 ± 156	226 ± 146	69 ± 41	52 ± 52	17 ± 17	798
Phyllocladus trichomanoides	-	-	-	-	-	0
Podocarpus totara	-	-	-	-	-	0
Prumnopitys ferruginea	2,569 ± 570	451 ± 170	347 ± 102	226 ± 94	52 ± 29	3,645
Prumnopitys taxifolia	69 ± 32	69 ± 54	87 ± 50	35 ± 24	-	260
Angiosperms						
Beilschmiedia tawa	6,354 ± 862	1,910 ± 448	2,431 ± 376	2,674 ± 692	469 ± 116	13,838

3.3.5. Vertical structure

Based on 510 height measurements covering all tree and tree fern species present, a set of 5 general height tiers was defined by the presence and dominance of species (Figure 40). Not all of these tiers were present everywhere, but they appeared in different combinations.

Figure 40. Typical 5-tier structure of the old-growth podocarp-broadleaved forest at the study site

Emergents (30 – 50 m)

The highest tier in the forests was dominated by scattered large-diameter podocarps and ranged from 30 m to 50 m. Tallest of them were *D. cupressinum* with a maximum of 48.9 m and *D. dacrydioides* with 48.6 m, being 10 m taller than the tallest *P. ferruginea* with 38.2 m. *Prumnopitys taxifolia* and *P. totara* had maximum heights of 35.6 and 35.4 m (Figure 41). Crowns of all emergent podocarps were disjunct with large gaps and dead upper crowns. It can therefore be inferred that those emergents had larger maximum heights in the past when crowns were intact. Dead standing podocarps of different diameter classes were encountered scattered throughout the forest.

Main canopy (20 – 30 m)

The height of the main canopy varied between plots. It was defined by a dense canopy of dominant mature *B. tawa* trees and ranged from c. 20 m to 30 m (Figure 42). Scattered mature and senescent trees of *E. dentatus* and *Knightia excelsa* were also present. Podocarps were generally absent from this tier.

Subcanopy (10 – 20 m)

Smaller tree species such as *W. racemosa, M. ramiflorus* and *P. crassifolius* form a subcanopy, even though these species did not occur in high densities. Instead, this tier was dominated mainly by *B. tawa* of 10 and 30 cm diameter. Other abundant species in the same diameter classes were *P. ferruginea* and *E. dentatus*. *Dacrydium cupressinum* and *D. dacrydioides* were found infrequently in the subcanopy.

Shrub tier (< 10 m)

The upper height limit of the tree fern *D. squarrosa* defined the height of the shrub layer (Figure 42). Other tree ferns such as *C. smithii* and *D. fibrosa* were also relatively frequent. Regeneration of angiosperm and gymnosperm tree species were other prominent features of this tier, as well as shrubs such as *C. dumosa*.

Ground layer

The forest floor was covered mainly by shed tree leaves. But several species of the fern genera *Asplenium*, *Blechnum*, *Polystichum* and *Hymenophyllum* were also present, in addition to seedlings of the various angiosperm and podocarp tree species. There was no indication of browsing limiting this layer.

3.3.6. Height modelling

Owing to the low abundance of many tree species, an extensive comparison of height growth was not possible. A strong correlation was observed between diameter and height in all species and the final model chosen for all tree species was the 3-parameter Korf function (Lundqvist, 1957).

Podocarps

Height-diameter modelling of podocarps *D. dacrydioides*, *D. cupressinum*, *P. ferruginea* and *P. taxifolia* was only possible to a limited extent due to the low number of individuals encountered (Figure 41). For *P. totara* only one measurement of 35.4 m was available for a single tree with a dbh of 178.7 cm. No other trees of that species were found at the study site. The problem was similar for *P. trichomanoides*, where only a single individual with a diameter of 26.8 cm and a height of 19.8 m was measured. But while *P. totara* was growing as an emergent tree, *P. trichomanoides* was a subcanopy tree. Emergent trees of *D. dacrydioides* ranged from 32.1 to 48.6 m height, with diameters from 95 to 202 cm. In the 8 additional plots that were established based on podocarp occurrence, another three trees of this species were measured and were smaller than 20 m with a maximum diameter of 29 cm. They were growing on a waterlogged site that was prone to flooding. Modelling emergent trees and subcanopy trees together did not produce any sensible results (see red dotted line in Figure 41). Therefore, the height-diameter relationship for the emergent trees was modelled separately. The same problems occurred for *D. cupressinum*. The middle diameter range from 25 to 77 cm was missing and also the height range from 19 to 28 m. In addition, emergent trees and subcanopy trees were found to show a different height-diameter relationship (see red dotted line in Figure 41). Both species were not present in the main canopy, as illustrated by the black horizontal dotted lines.

A similar distribution was evident for *P. ferruginea*, where diameters ranged from 7.2 to 100.2 cm, but diameters between 27.9 and 63.7 cm were completely missing. This corresponds to trees of heights between 18.6 and 26.2 m and means that this species was also only found in the subcanopy and in the emergent tier. But separate height modelling for both tiers did not result in major differences. Only seven individuals of *P. taxifolia* were found and with diameters ranging from 84 to 146 cm these covered heights from 24.4 to 35.6 m. This means that this species was found in the emergent tier as well as in the main canopy. But here the relationship between dbh and height was not as clear as for *D. cupressinum* and *P. ferruginea*. However, missing heights in the lower diameter classes in combination with low numbers of measurements charge the height curve models with potentially large errors.

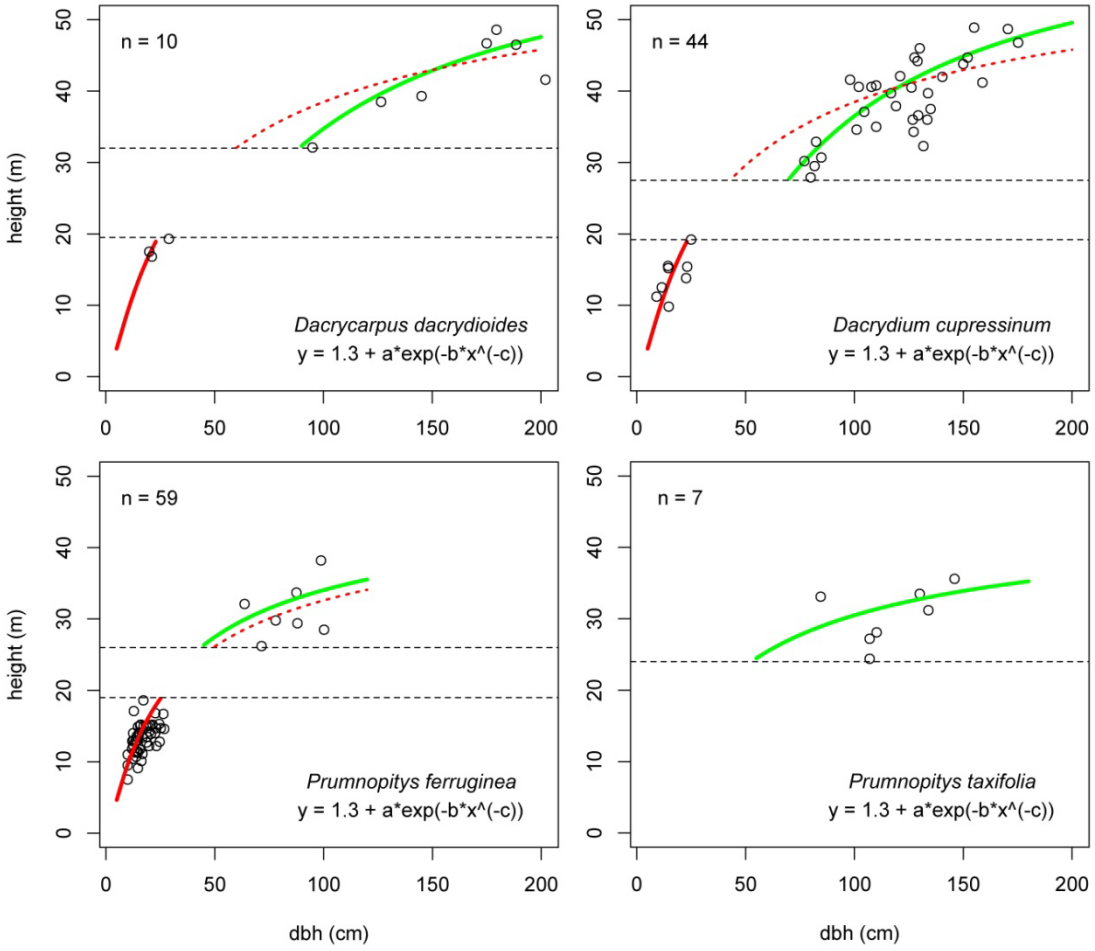

Figure 41. Height/dbh curves for *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Prumnopitys taxifolia* at the study site. The green lines are the height curves for the emergent trees, while the red lines include all trees. The area between the dotted lines indicates the main canopy.

Angiosperms

Of the 15 angiosperm tree species and 4 tree fern species, only 6 species occurred in sufficient numbers for height modelling (Figure 42). *Beilschmiedia tawa* was the most abundant tree species in the main canopy and subcanopy with heights between 8.3 and 33.5 m, covering all diameter classes. *Elaeocarpus dentatus* was not found to reach that height, with 27.5 m being the largest measured individual of that species. But while this species was abundant in the subcanopy, only scattered individuals were found in the main canopy. For *E. hookerianus* and *N. lanceolata*, only subcanopy trees between 10 and 16 m height were found. But the numbers of individuals of those species were generally low. This was also the case for *K. excelsa*. But it occurred in the subcanopy as well as the canopy with heights from 13.4 to 28.5 m.

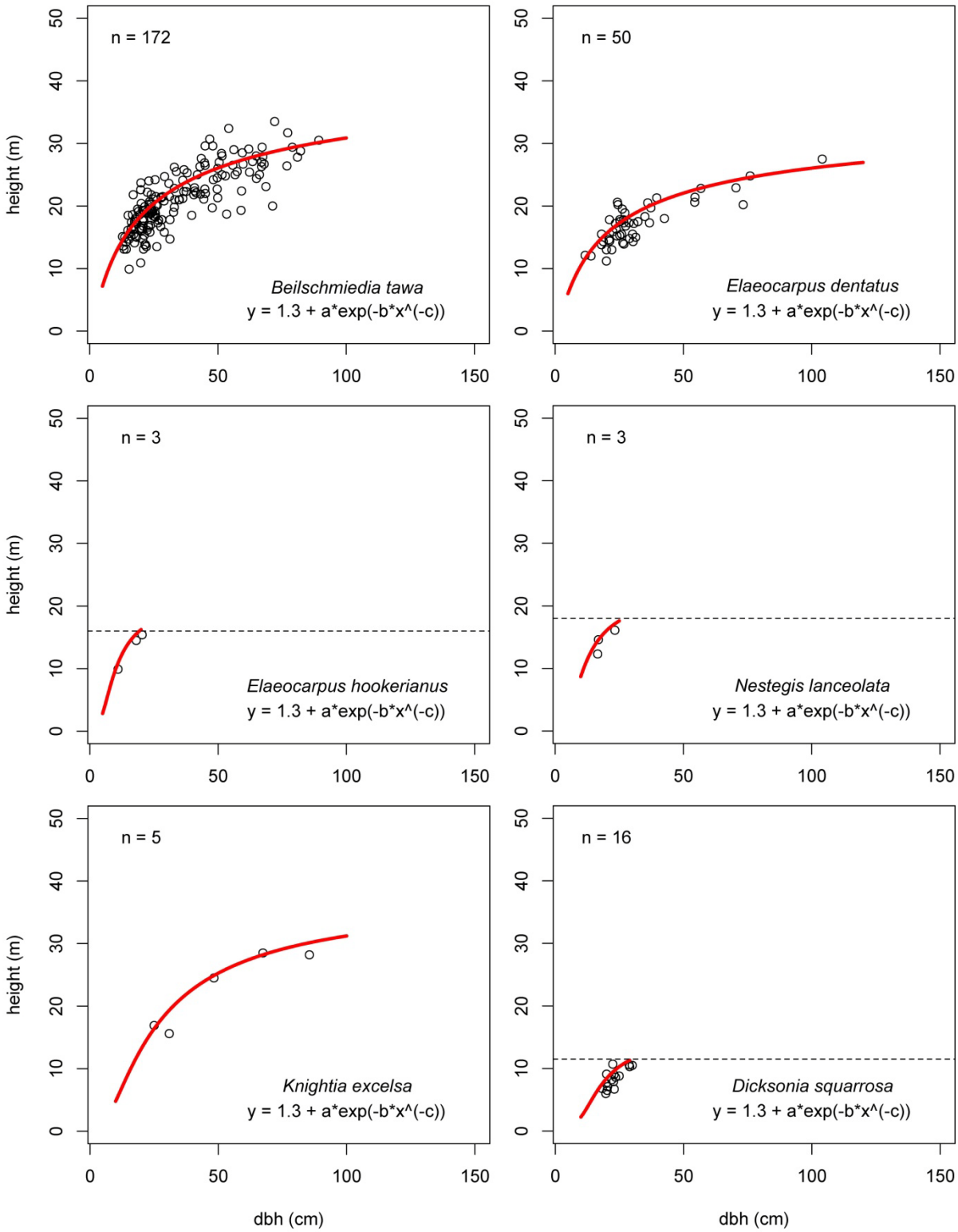

Figure 42. Height/dbh curves for angiosperms *Beilschmiedia tawa* (non-linear regression), *Elaeocarpus dentatus* (polynomial regression), *Elaeocarpus hookerianus* (non-linear regression), *Nestegis lanceolata* (non-linear regression), *Knightia excelsa* (non-linear regression) and the tree fern *Dicksonia squarrosa* (non-linear regression) at the study site. The dotted lines show upper limits of measured heights.

Tree ferns

Tree ferns were found throughout the shrub tier with *D. squarrosa* being the tallest species. Heights of 19.7 to 22.4 cm diameter individuals ranged from 6.0 to 10.7 m. Height-diameter modelling was not undertaken for these as they do not add on diameter growth as they grow taller.

Podocarps and *Beilschmiedia tawa*

Plotting all height and diameter measurements of all podocarps and the measurements for all *B. tawa* of the main canopy in one diagram reveals a graphic correlation between those species (Figure 43). Podocarps are generally absent in the main canopy which was occupied almost exclusively by *B. tawa*. Only a few individuals of large diameter podocarps were growing in that tier, in particular at the upper limit of the main canopy, where only few *B. tawa* were found.

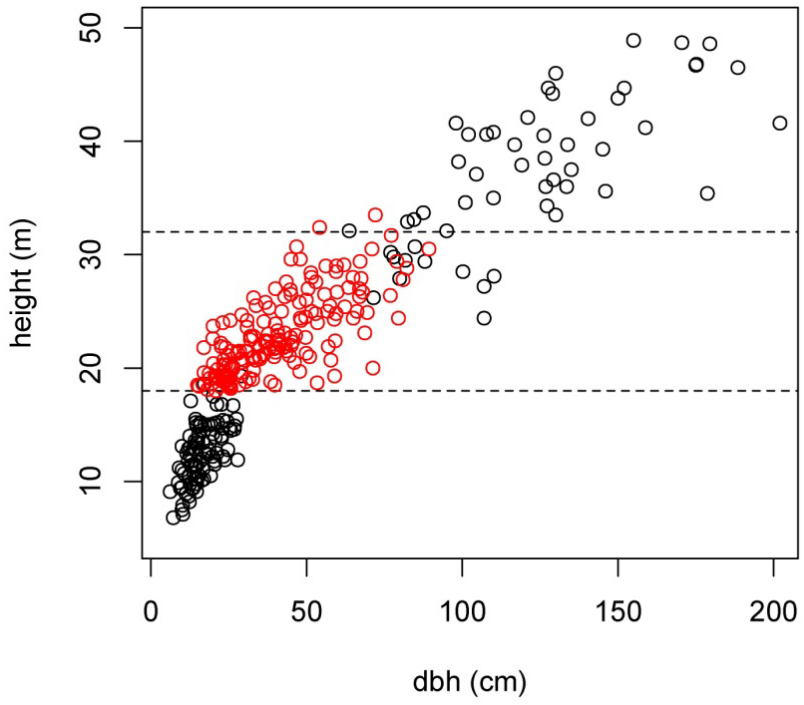

Figure 43. Height and diameter measurements of all podocarps (black) in comparison to measurements of *Beilschmiedia tawa* (red) in the main canopy (dotted lines = main canopy ± 2 m)

3.3.7. Social class

Due to the low frequency and density of podocarp species in the circular plots, there were not enough trees to investigate the relationship between social class and height. Therefore, 8 additional samplings points were established at sites where subcanopy podocarps are present and circular plots were set up the same way as at the random sampling points with the same variables being recorded, leading to a total of 121 podocarps sampled. Based on 355 height measurements, the relationship between social class and tree height was evaluated for the 6 podocarp species (Figure 44) as well as for 4 angiosperm species (Figure 45). The only trees found in class 1 were emergent individuals of *D. dacrydioides*, *D. cupressinum*, *P. ferruginea* and *P. taxifolia* with diameters < 60 cm, with *P. totara* and *P. taxifolia* not being present in any other class. No podocarps were found to be dominant in the main canopy (class 2) but 35 % of the sampled podocarps were codominant trees in this canopy. All non-emergent *D. dacrydioides* and *P. trichomanoides* appeared only as codominant canopy trees in class 3 with heights just under 20 m.

D. cupressinum showed a distinctive height difference between class 3 and class 4 trees. This was not apparent for *P. ferruginea* which also occurred in both classes. None of the podocarps of class 3 faced any direct competition from class 2 trees but only competed with angiosperms of class 3.

B. tawa was the most abundant tree species in class 2 with heights ranging from 18.7 to 33.5 m. The only other tree species being dominant in the main canopy was *E. dentatus*, while only a single individual of *K. excelsa* was found in that class. In the social classes 3 and 4, *B. tawa* was also the most abundant tree species with heights between 10.9 and 25.8 m, followed by *E. dentatus*. *N. lanceolata* and *K. excelsa* played only a minor role in class 3 and were completely missing in any lower class.

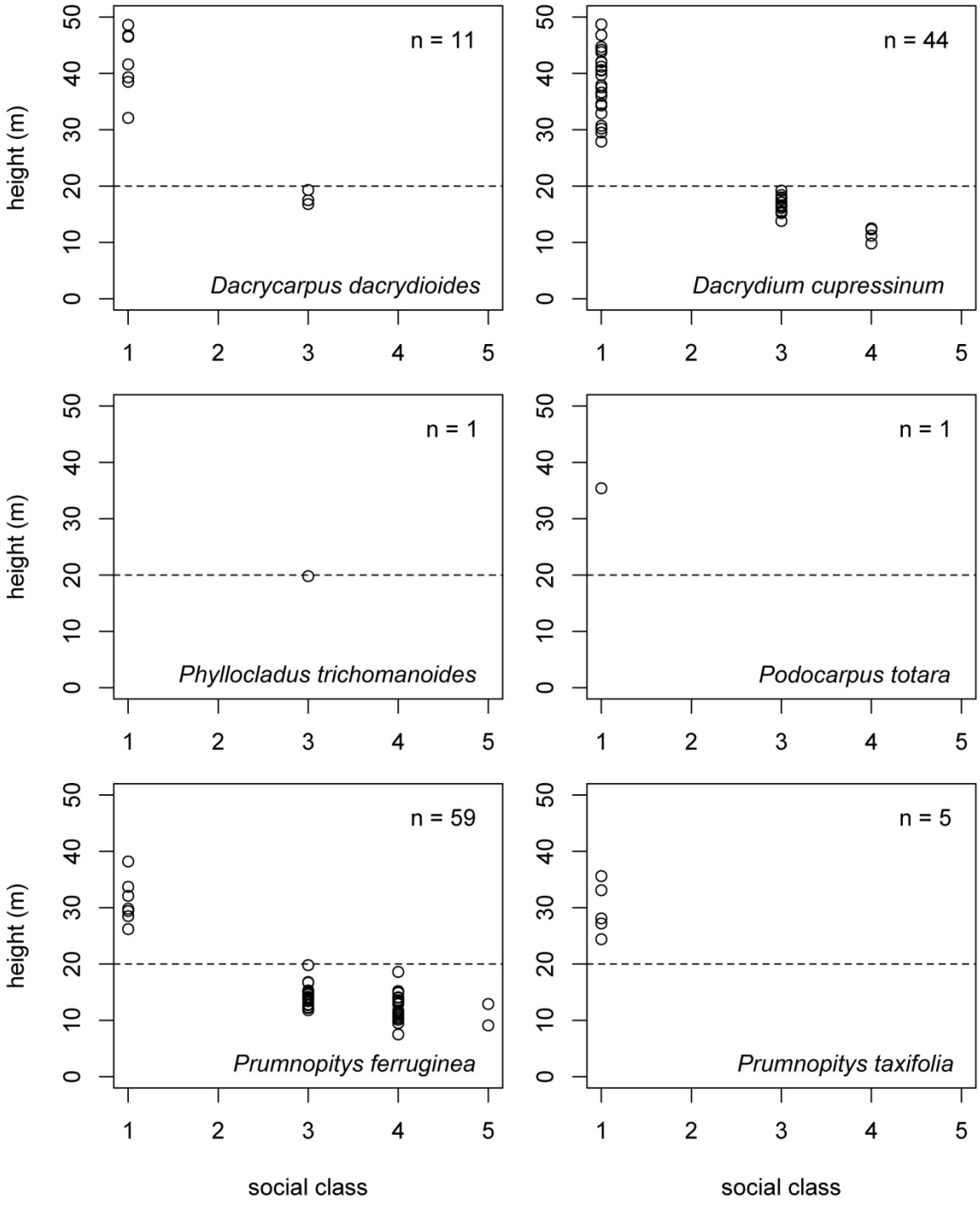

Figure 44. Relationship between social class and height of 6 podocarp species; the dotted line reflects the general intersection between canopy and subcanopy

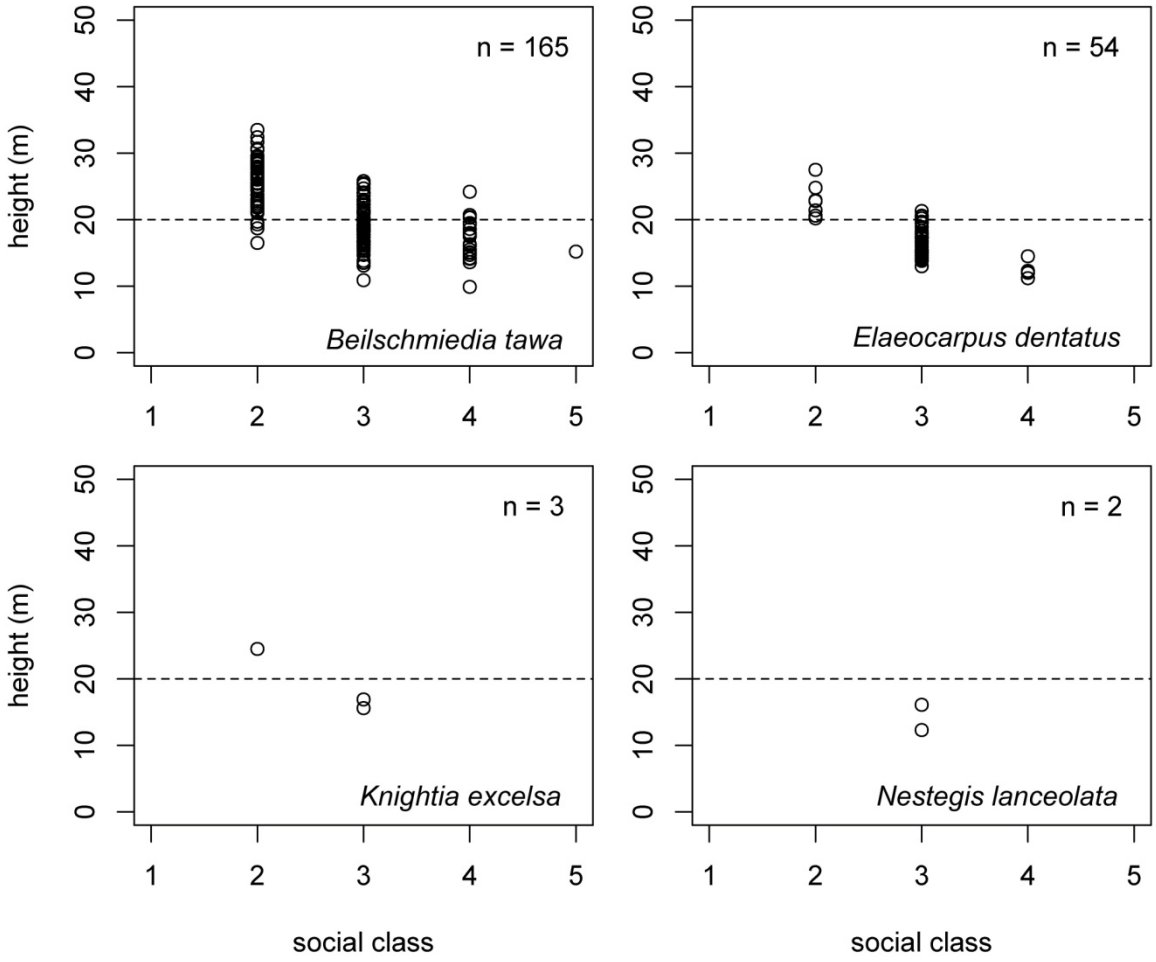

Figure 45. Relationship between social class and height of 4 angiosperm canopy species; the dotted line reflects the general intersection between canopy and subcanopy

3.3.8. Age structure

For the age structure analysis, the set of random plots was used in combination with the additional plots that were selected based on their presence of podocarps. This way, more species and diameters could be sampled, in particular of *D. dacrydioides* and *P. trichomanoides*. The podocarps *P. totara* and *P. taxifolia* were, however, still not represented by those additional plots and no further trees were found at the study site.

Diameters of podocarps at the study site could be divided into two main groups: trees with dbh < 30 cm and trees with dbh > 70 cm. Sounding of all trees of the second group returned either characteristic positive signs of internal decay or did not return any clear results. With heart rot making ageing extremely difficult and to prevent further potential decay or infection, no tree of this group was cored.

Diameter/age relationship

The diameters of sampled podocarps ranged from 9.1 to 35.2 cm covering an age span from 52 to 249 years (Figure 46). Their mean age was 87 years (SE = 2.29, SD = 18.6), ranging from 80 yrs for *D. cupressinum,* 88 years for *P. ferruginea* and 93 years for *P. trichomanoides* to 99 years for *D. dacrydioides*. Trees with diameters > 30 cm were rare (3 %) and most trees were younger than 100 years (78 %). Here, the only exception was *P. ferruginea*, where 98 % of the trees were between 57-147 years old. The majority of trees within the 10-30 cm diameter range of all podocarps (80 %) were between 60 and 100 years old. There was a significant positive correlation ($p < 0.05$) between age and diameter of *P. ferruginea* and a model comparison based on an AIC test of linear and non-linear models returned a polynomial model that explained 34 % of the variation.

A single individual of D. cupressinum showed an extremely high age of 249 years with a diameter of only 25.0 cm. A similar slow growing example was found in *P. ferruginea*, where a single individual was estimated to be 207 years old with a diameter of 31.9 cm. This relationship was in accordance with the modelled relationship of age and diameter in *P. ferruginea*, while it was an outlier in *D. cupressinum*.

Beilschmiedia tawa and *E. dentatus* trees that were larger than 40 cm were often found to be affected by internal decay and could therefore not be cored. But with the additional plots included into this study, 12 trees of *B. tawa* and 1 tree of *E. dentatus* of those larger dimensions could be sampled.

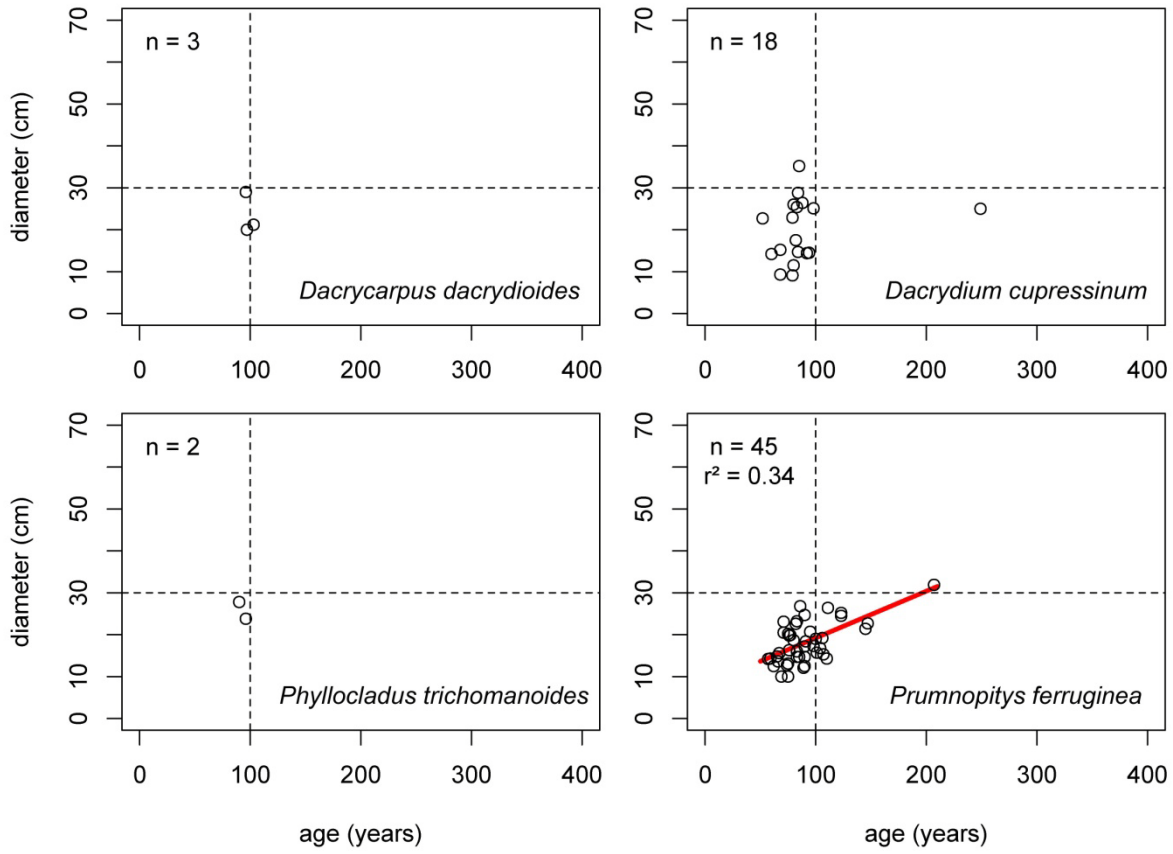

Figure 46. Diameter/age relationship of four podocarp species

Beilschmiedia tawa and *E. dentatus* showed a significant positive correlation between diameter and age (Figure 47). The diameters of *B. tawa* ranged from 12.8 to 66.2 cm, representing almost the whole diameter distribution of that species. The age span ranged from 47 to 358 years. But with 80% of the trees between 10 and 30 cm diameter being between 104 and 217 years old, these trees were around twice as old as the podocarps of similar diameters. *E. dentatus* showed a diameter/age distribution that is similar to the podocarps with 80 % of the sampled trees being between 50 and 100 years old. But within that age range, trees had generally larger diameters than the podocarps.

Modelling the diameters of 100 year old trees showed that *E. dentatus* (28.4 cm) was the tree species with the largest diameter growth of the three modelled species, while the growth of *P. ferruginea* (19.2 cm) and *B. tawa* (19.5 cm) was very similar.

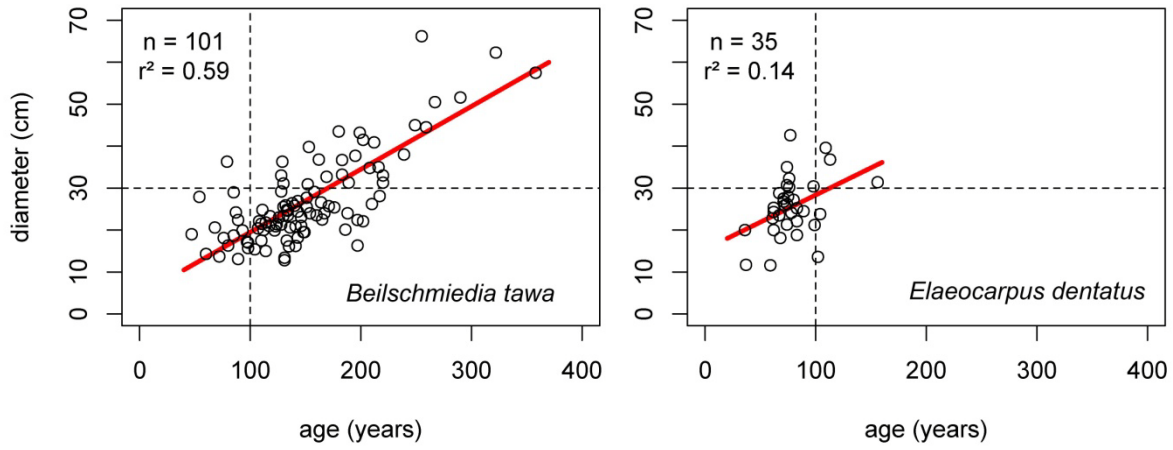

Figure 47. Diameter/age relationship of *Beilschmiedia tawa* and *Elaeocarpus dentatus*

Height/age relationship

The mean height growth of trees within the same class was found to vary considerably, with higher social classes growing faster than lower social classes. An exception was *B. tawa*, where the height growth of dominant trees of class 2 was lower than that of codominant and subdominant classes (Table 26). The age range within social classes was also found to be very large, ranging from 47-259 years in the case of codominant *B. tawa* and from 62-207 years in case of *P. ferruginea*.

Table 26. Relationship between mean annual height growth of 6 tree species and social classes 2-5 based on 204 tree cores as an indication for mean annual height growth (m yr^{-1}); species mean in brackets

Gymnosperms	**2**	**3**	**4**	**5**
Dacrycarpus dacrydioides	-	0.16 – 0.20 (0.18)		
Dacrydium cupressinum	-	0.08 – 0.27 (0.19)	0.12 – 0.18 (0.15)	
Phyllocladus trichomanoides	-	0.22 [*n* = 1]		
Prumnopitys ferruginea	-	0.10 – 0.21 (0.15)	0.10 – 0.24 (0.16)	0.11 – 0.14 (0.13)
Angiosperms				
Beilschmiedia tawa	0.07 – 0.21 (0.11)	0.06 – 0.41 (0.15)	0.08 – 0.23 (0.14)	0.11 – 0.11 [0.11]
Elaeocarpus dentatus	-	0.10 – 0.36 (0.22)	0.14 – 0.33 (0.21)	

All measured podocarps had heights < 20 m, which is lower than the height of the main canopy (Figure 48). As only one *P. trichomanoides* (19.8 m) was measured, no further modelling could be carried out for this species. A similar problem was encountered with *D. dacrydioides* where only three trees of heights between 18.8 and 19.3 m were sampled.

Trees of both species were close to 100 years old. The heights of *D. cupressinum* ranged from 9.8 to 19.2 m with an age range of 52 to 98 years. Owing to the small age range of 46 years in relationship to the large height variation, no further analysis could be carried out for this species either. In addition, one tree showed extremely slow growth with a height of only 19.2 m at an age of 249 years and a diameter of 25.0 cm. *Prumnopitys ferruginea* was the only podocarp species that occurred in numbers that allowed further modelling. Here, height measurements ranged from 7.5 to 18.6 m in the age range from 50 to 150 years and the relationship was found to be significant positive for that period. One tree, however, was 207 years old and had a height of only 19.8 m and a diameter of 31.9 cm. The relationships between age and height for *D. dacrydioides*, *D. cupressinum* and *P. trichomanoides* are only displayed for comparison.

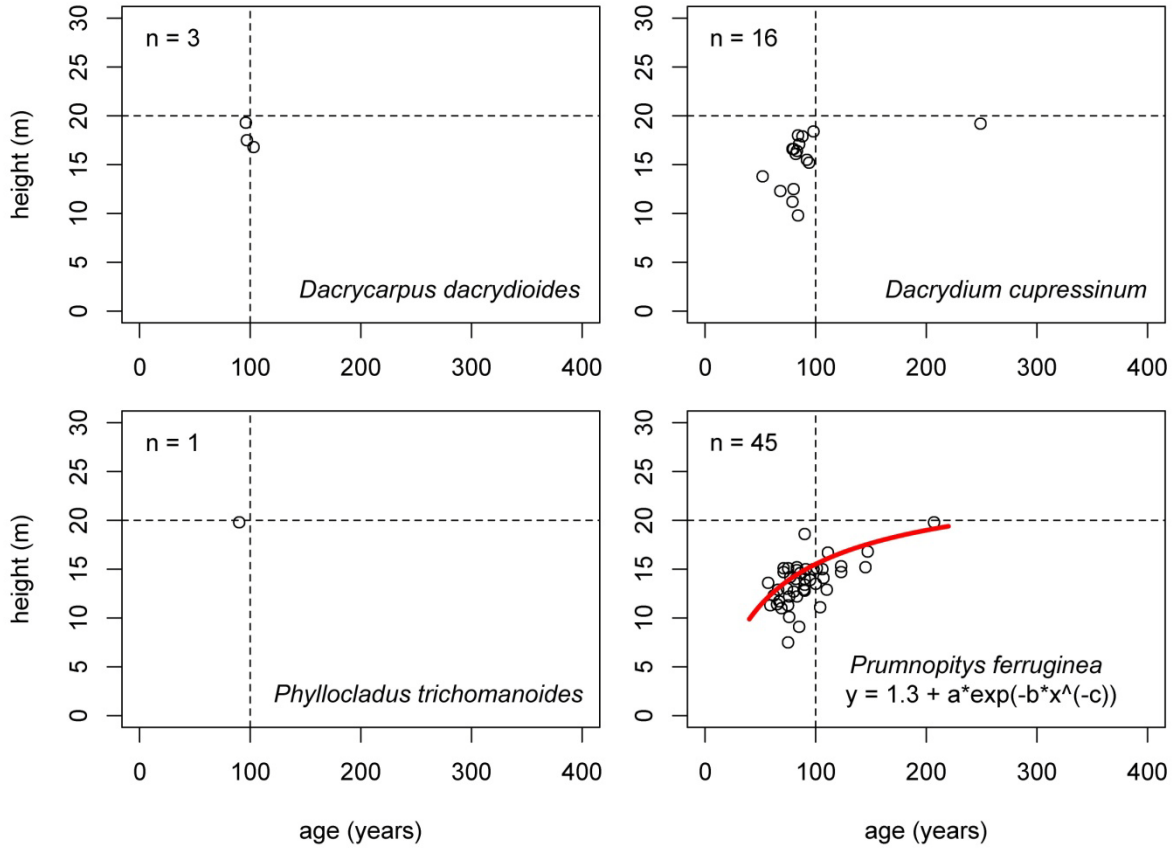

Figure 48. Height/age relationship of four podocarp species

Height measurements of *B. tawa* ranged from 9.9 to 27.6 m and of *E. dentatus* from 11.2-21.3 m. Modelling of the relationship between height growth and age showed a strong positive correlation for *B. tawa* and *E. dentatus* (Figure 49). A comparison of modelled

heights for 80 year old trees of *P. ferruginea*, *B. tawa* and *E. dentatus* showed that *P. ferruginea* had with 14.2 m the shortest height, while *B. tawa* was with 17.9 m the tree species with the tallest height, followed by *E. dentatus* with 17.5 m.

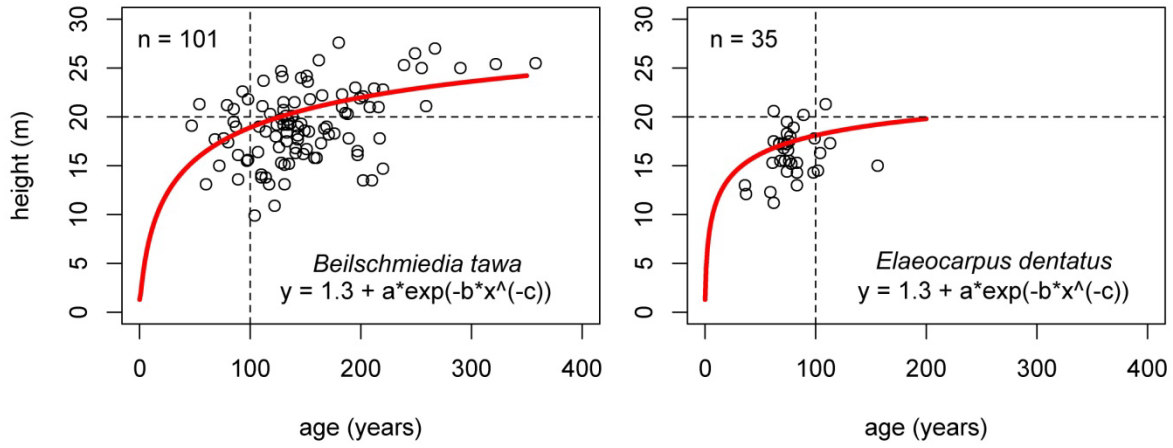

Figure 49. Height/age relationship of *Beilschmiedia tawa* and *Elaeocarpus dentatus*

3.3.9. Diameter growth analysis

All 4 podocarp species showed very slow diameter growth with an overall mean of 2.2 mm yr^{-1}, but growth varied slightly between species (Table 27). While *P. trichomanoides* was the podocarp species with the largest mean growth, *D. cupressinum* showed the largest range in growth and represented the slowest and fastest growing podocarp trees. The overall fastest growing tree species was *E. dentatus,* which grew on average almost twice as fast as *B. tawa*, the species with the slowest overall diameter growth.

Table 27. Mean annual diameter growth (*mai*) of different tree species based on tree cores (full life-span)

Species	range (mm yr^{-1})	mean	SE	SD
Dacrycarpus dacrydioides	2.1 – 3.0	2.4	0.3	0.6
Dacrydium cupressinum	1.0 – 4.4	2.4	0.2	1.0
Phyllocladus trichomanoides	2.5 – 3.1	2.8	0.3	0.4
Prumnopitys ferruginea	1.3 – 3.3	2.1	0.1	0.5
all podocarps	1.1 – 4.4	2.2	0.1	0.7
Beilschmiedia tawa	0.8 – 5.2	1.9	0.1	0.7
Elaeocarpus dentatus	1.3 – 5.6	3.4	0.2	0.9

But growth varied not only between species, but also between different social classes within a species (Table 28). A comparison of the mean increment over the past 50 years for the different species in focus shows that *E. dentatus* was again the fastest growing species in all classes. But *D. dacrydioides* was the fastest growing podocarp species in class 3 within that time period, followed by *D. cupressinum* and *P. ferruginea*. *Phyllocladus trichomanoides* on the other hand, even though it appeared to be the fastest growing species when the whole life-span of every tree was taken into account, was in social class 3 the species with the smallest diameter increment of all sampled species. Generally, trees of higher social classes showed a faster mean growth than trees of lower social classes of the same species. The only exception was *B. tawa*, where dominant trees of the main canopy (class 2) showed a lower mean increment than the codominant trees of class 3.

Table 28. Mean annual diameter growth (*mai*) over 50 years (mm yr^{-1}) ± one standard error of different tree species and social classes (1-5) based on 195 tree cores

Gymnosperms	**1**	**2**	**3**	**4**	**5**
Dacrycarpus dacrydioides	-	-	4.0 ± 0.5	-	-
Dacrydium cupressinum	-	-	3.1 ± 0.3	2.2 ± 0.2	-
Phyllocladus trichomanoides	-	-	2.8 ± 0.3	-	-
Prumnopitys ferruginea	-	-	2.9 ± 0.2	2.3 ± 0.1	2.3 ± 0.2
Angiosperms					
Beilschmiedia tawa	-	2.5 ± 0.3	2.9 ± 0.1	2.5 ± 0.2	-
Elaeocarpus dentatus	-	-	4.2 ± 0.2	2.7 ± 0.6	-

The findings of *B. tawa* led to the assumption that the annual increment might correlate not only with social class but also with the age of a tree, where older trees have a slower radial increment than younger trees. Therefore the mean annual increment was calculated for every tree for the past 50 years and tested as a response variable against their age (Figure 50). But as an insufficient age range of trees of the species *D. dacrydioides*, *D. cupressinum*, *P. trichomanoides* and *E. dentatus* was covered, the analysis could be carried only out for *P. ferruginea* and *B. tawa*. Here, only *B. tawa* showed a significant relationship between diameter increment and age. But all species showed a large variation of diameter growth between trees of similar age and the explanatory value of the models used was low ($r^2 < 0.1$) for all models tested. Including the social class into the model did not return any significant improvement based on an AIC model comparison.

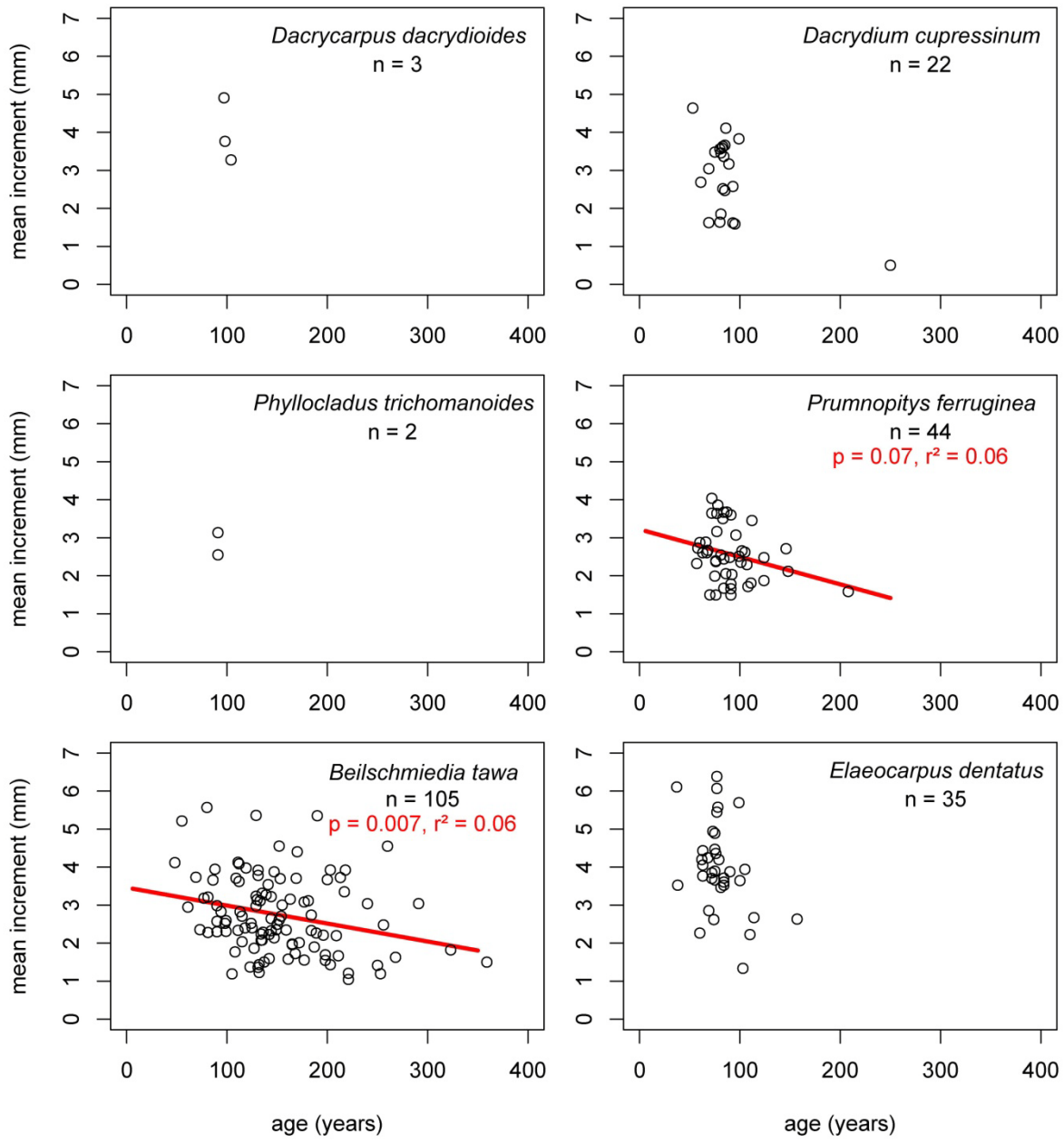

Figure 50. Relationship between the mean annual diameter growth (*mai*) of the past 50 years and the age of trees for 6 different sampled species

Diameter growth differed not only between trees of the same species but also varied between different years within a tree. A comparison of the widest and narrowest ring of every podocarp tree shows that all trees had a considerable range of radial increment of factors 8-16 (Figure 51). This range, as well as the absolute values of radial increment, did not seem to be related to the social class of a tree and the variations in those ranges appeared larger within species than between species. The results also show that the diameter growth between different species as well as between different social classes of the

same species was quite similar with a maximum growth between 7 and 10 mm yr^{-1}. However, low sample sizes and an under-representation of social classes precluded a more detailed analysis.

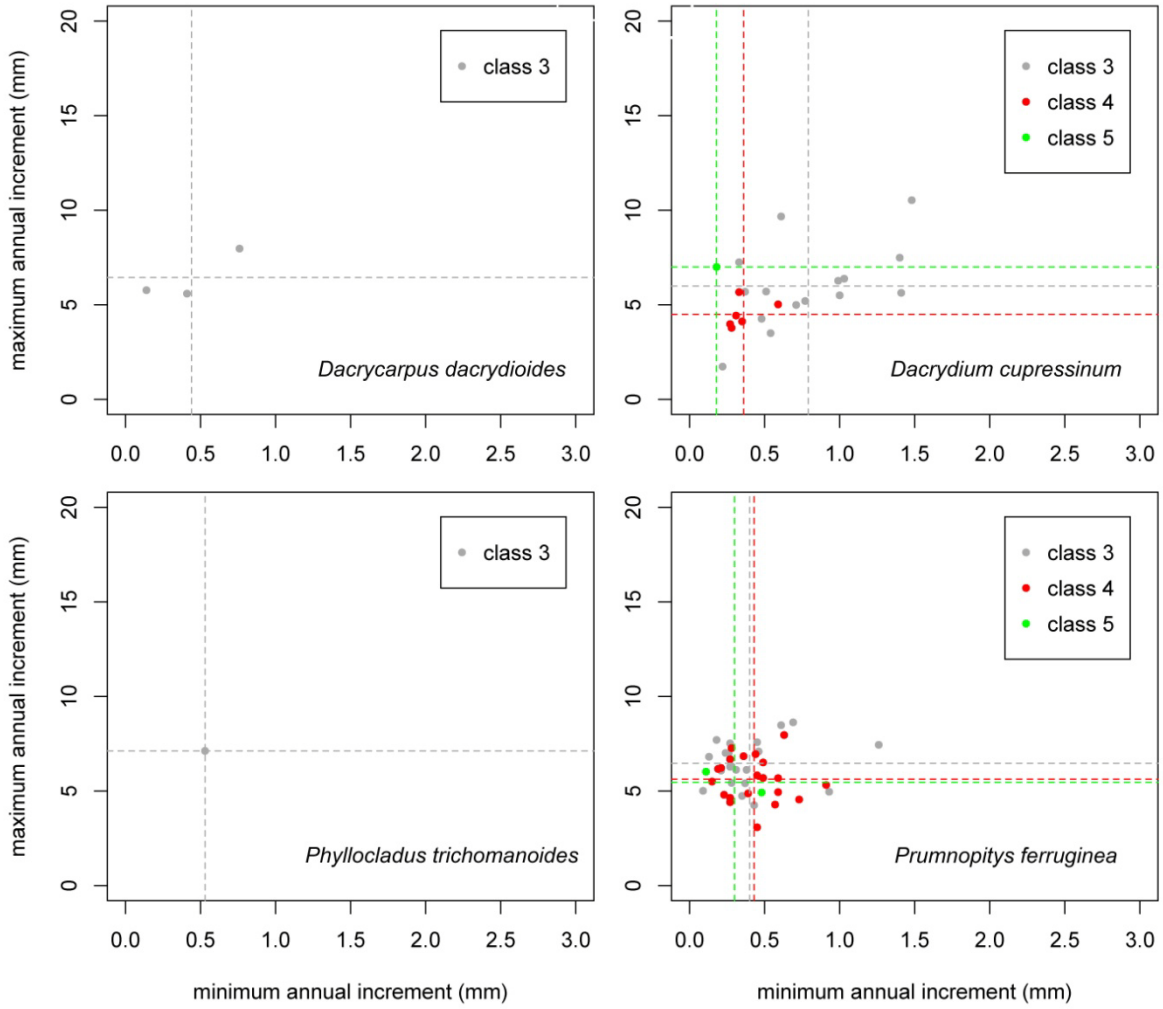

Figure 51. Maximum and minimum annual radial increment of trees of different podocarp species and social classes; the dashed lines show the means of the minima and maxima for each social class

This variation in diameter growth was also found in the sampled angiosperm tree species, where it was much larger for *E. dentatus* than for *B. tawa* (Figure 52), the latter species generally growing more slowly. The differences between minimum and maximum growth, however, ranged from factors 13-15 for *E. dentatus* to factors 28-30 for *B. tawa* for the different social classes. *B. tawa* trees of all social classes were found to grow extremely slowly at times, representing the slowest growing species of all. But it was also able to grow

as fast as the podocarps and even faster. But again, most social classes were under-represented in any other species than *B. tawa*, precluding more detailed analysis.

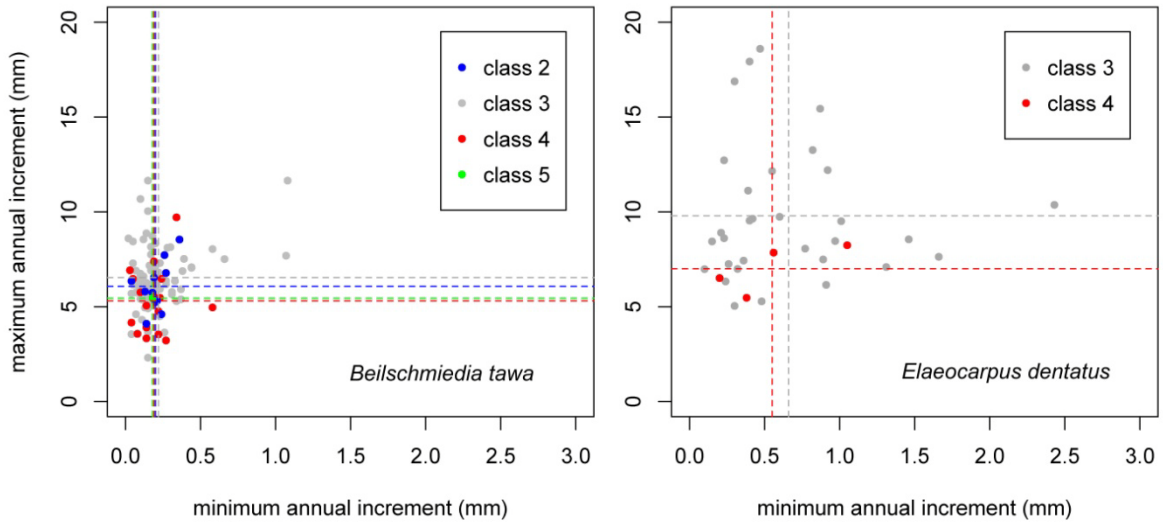

Figure 52. Maximum and minimum annual radial increment of trees of different angiosperm species and social classes; the dashed lines show the means of the minima and maxima for each social class

A complete overview of minimum and maximum annual diameter increment for the different tree species and social classes is given in Table 29. The tree species with the fastest annual increment was again *E. dentatus* with a maximum of 18.6 mm yr^{-1} in class 3 and an overall mean maximum of 9.48 mm yr^{-1}. But also *B. tawa* was able to grow up to 11.65 mm yr^{-1}, faster than any sampled podocarp tree, even though the mean maximum growth was with 6.27 mm yr^{-1}, similar to that of the podocarps. As already mentioned above, *B. tawa* was also the tree species with the slowest diameter growth where tree rings were found to be as little as 0.02 mm apart. However, this species' mean minimum was with 0.21 mm yr^{-1}, 10 times higher than its absolute minimum. This extremely slow growth was again not related to the social class of a tree but was found within trees of all classes. While *E. dentatus* was the fastest growing tree species, it could also grow as slow as 0.1 mm yr^{-1}, even though this was not common with a mean minimum of 0.65 mm yr^{-1}.

Among the podocarps, *D. cupressinum* was with 10.53 mm yr^{-1} the fastest growing species and was the only podocarp species growing more than 10 mm yr^{-1}. The mean maximum growth, however, was with 5.63 mm yr^{-1}, slower than any other podocarp species. The maximum growth of the other podocarp species ranged from 7.12 to 8.63 mm yr^{-1}. The

podocarp species showing the smallest annual minimum diameter growth was *P. ferruginea* with 0.09 mm yr^{-1}, and even the mean minimum growth of 0.41mm yr^{-1} was slower than that of any other podocarp species.

Table 29. Annual diameter increment (mm) of trees of different species and social classes with mean (± One Standard Error), standard deviation and range

Social class	Annual increment		*Dacrycarpus dacrydioides*	*Dacrydium cupressinum*	*Phyllocladus trichomanoides*	*Prumnopitys ferruginea*	*Beilschmiedia tawa*	*Elaeocarpus dentatus*
class 2	minimum	mean					0.22 ± 0.03	
		SD					0.08	
		range					0.04 – 0.36	
	maximum	mean					6.07 ± 0.39	
		SD					1.31	
		range					4.10 – 8.54	
class 3	minimum	mean	0.44 ± 0.18	0.79 ± 0.11	0.53 (*n* = 1)	0.40 ± 0.06	0.22 ± 0.02	0.66 ± 0.09
		SD	0.31	0.41		0.28	0.19	0.52
		range	0.14 – 0.76	0.22 – 1.48		0.09 – 1.26	0.02 – 1.08	0.10 – 2.43
	maximum	mean	6.44 ± 0.77	5.99 ± 0.57	7.12 (*n* = 1)	6.47 ± 0.27	6.54 ± 0.19	9.80 ± 0.64
		SD	1.33	2.20		1.22	1.67	3.58
		range	5.59 – 7.97	1.73 – 10.53		4.25 – 8.63	2.31 – 11.65	5.04 – 18.60
class 4	minimum	mean		0.36 ± 0.05		0.43 ± 0.04	0.19 ± 0.03	0.55 ± 0.18
		SD		0.12		0.20	0.13	0.37
		range		0.27 – 0.59		0.15 – 0.91	0.03 – 0.58	0.20 – 1.05
	maximum	mean		4.50 ± 0.29		5.63 ± 0.26	5.31 ± 0.18	7.02 ± 0.64
		SD		0.72		1.18	1.67	1.27
		range		3.78 – 5.67		3.08 – 7.96	3.22 – 9.71	5.47 – 8.24
class 5	minimum	mean		0.18 (*n* = 1)		0.30 ± 0.19	0.18 (*n* = 1)	
		SD				0.26		
		range				0.11 – 0.48		
	maximum	mean		7.00 (*n* = 1)		5.47 ± 0.55	5.45 (*n* = 1)	
		SD				0.78		
		range				4.92 – 6.02		
all classes	minimum	mean	0.44 ± 0.18	0.64 ± 0.09	0.53 (*n* = 1)	0.41 ± 0.04	0.21 ± 0.02	0.65 ± 0.08
		SD	0.31	0.41		0.24	0.17	0.5
		range	0.14 – 0.76	0.18 – 1.48		0.09 – 1.26	0.02 – 1.08	0.1 – 2.4
	maximum	mean	6.44 ± 0.77	5.63 ± 0.42	7.12 (*n* = 1)	6.02 ± 0.19	6.27 ± 0.16	9.48 ± 0.59
		SD	1.33	1.97		1.24	1.68	3.5
		range	5.59 – 7.97	1.73 – 10.53		3.08 – 8.63	2.31 – 11.65	5.04 – 18.60

Variations in diameter growth within individual trees were found to generally be clustered, with groups of small rings followed by groups of large rings and vice versa. This general pattern of sudden increase or decreases of annual increment was found in all species (Table 30). In particular, releases after phases of initial slow growth were observed in more than 80 % of trees. The only exception was *E. dentatus*, where only 56 % of trees showed such a release. Relating those release phases to the age of trees showed that *D. dacrydioides* and *D. cupressinum* had more releases per year than any other species. Here, all other sampled species showed similar values between 0.009 and 0.011 releases per year.

Phases of suppression were less common in sampled trees. In *P. ferruginea*, *D. cupressinum* and *B. tawa*, phases of suppression were observed in almost 50 % less trees than releases. Results for *E. dentatus* were again different to all other species, as numbers of trees with suppression were identical to the numbers of trees with release.

Table 30. Percentage of species that showed phases of release and suppression and the calculated mean releases and mean suppressions per year.

Gymnosperms	***n***	**release**	**release yr^{-1}**	**suppression**	**suppression yr^{-1}**
Dacrycarpus dacrydioides	3	100 ± 0	0.023 ± 0.004	0 ± 0	0 ± 0
Dacrydium cupressinum	22	95 ± 5	0.017 ± 0.002	55 ± 11	0.007 ± 0.002
Phyllocladus trichomanoides	1	100 ± 0	0.011 ± 0.000	100 ± 0	0.011 ± 0.000
Prumnopitys ferruginea	44	82 ± 6	0.011 ± 0.001	41 ± 7	0.005 ± 0.001
Angiosperms					
Beilschmiedia tawa	105	91 ± 3	0.010 ± 0.001	47 ± 5	0.004 ± <0.001
Elaeocarpus dentatus	36	56 ± 8	0.009 ± 0.001	56 ± 8	0.008 ± 0.001

While phases of release in time were evident mostly in individual trees, there were also phases that were shared by multiple trees within the study site (Figure 53). One such phase was the period between 1936 and 1945 where sampled trees of every species showed the highest number of releases for the past 200 years.

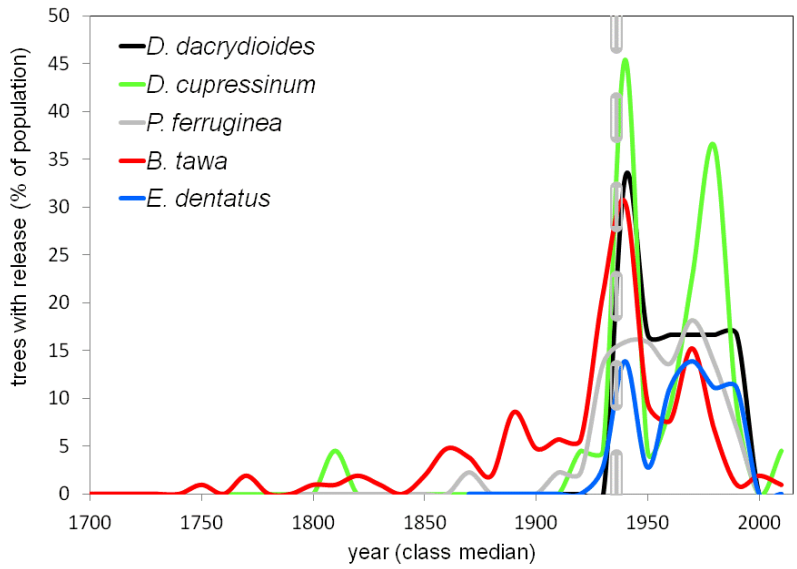

Figure 53. Phases of release shared by different trees of the same species; values on the x-axis are 10-year-classes, while the class midpoints are displayed. The grey vertical dashed line depicts the year 1936.

Forty-seven % of the cored trees were less than 20 years of age (at coring height in 0.2 m) at the beginning of the release in 1936. In addition, the numbers of young trees that successfully established in the course of the release event increased noticeably, in particular for *E. dentatus* (61 %) and *P. ferruginea* (39 %) (Figure 54).

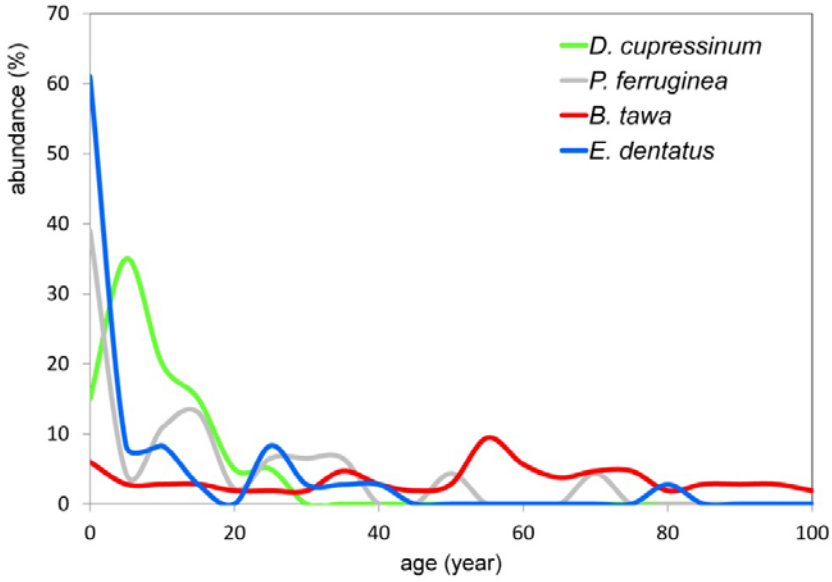

Figure 54. Abundance of sampled trees in different age classes at the time of the release in 1936

These young trees were, according to their calculated diameters, still seedlings in 1936 (Table 31). In particular, sampled trees of *E. dentatus* (90 %) and *D. cupressinum* (80 %) showed their highest abundance in that class while *B. tawa* (17 %) was the species with the lowest abundance of young trees.

Table 31. Proportion (%) of total sampled trees (*n*) that were less than 20 years of age at coring height in 1936 with minimum, maximum and mean diameters (± one SE) in 1936

Gymnosperms	**%**	**mean diameter in 1936 (cm)**	**min/max diameter in 1936 (cm)**	**total *n***
Dacrycarpus dacrydioides	67	1.6 ± 0.7	0.9 – 2.4	3
Dacrydium cupressinum	90	0.8 ± 0.2	0.0 – 2.9	20
Phyllocladus trichomanoides	100	1.6 ± 0.0	1.6 – 1.6	1
Prumnopitys ferruginea	32	0.5 ± 0.1	0.0 – 2.0	46
Angiosperms				
Beilschmiedia tawa	17	1.1 ± 0.3	0.0 – 5.0	106
Elaeocarpus dentatus	80	0.3 ± 0.1	0.0 – 2.4	36

On the other hand, phases of suppression occurred mainly on individual or small group basis (Figure 55) but an increase of trees with suppression since 1950 is evident, in particular for *D. cupressinum*, *P. ferruginea* and *E. dentatus*, culminating at close to 30 % in recent years for *D. cupressinum* and *E. dentatus*.

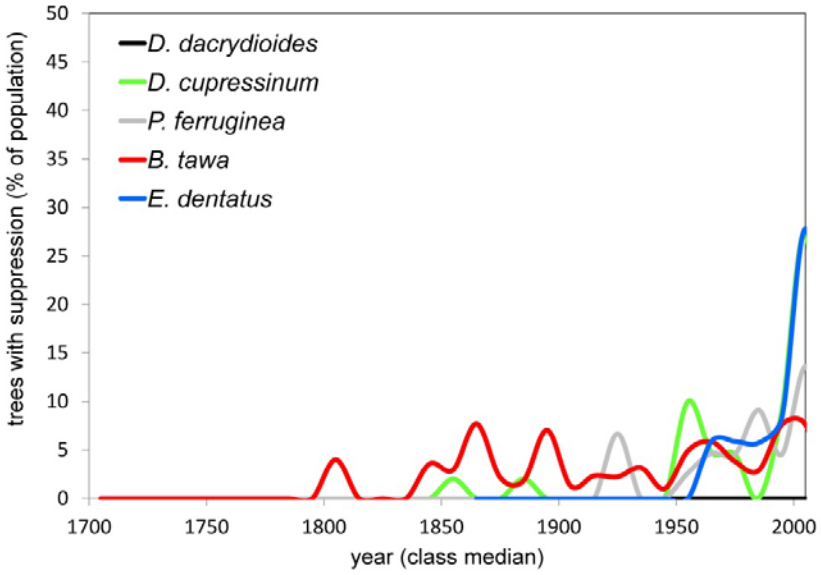

Figure 55. Phases of suppression shared by different trees of the same species; values on the x-axis are 10-year-classes, while the class midpoint is displayed.

3.3.10. Mortality

In 1959, all merchantable podocarps were tagged and measured. Subsequently, all those trees being still alive were re-tagged and re-measured in 2002. The differences in numbers of measured trees of the different species show that 30 % of the tagged trees had died over the period of 43 years (Table 32). *Prumnopitys ferruginea* was the species with the highest mortality (40 %), followed by *D. cupressinum* (31 %) and *P. taxifolia* (29 %). These were the species with the highest abundance in the emergent tree class. *Dacrycarpus dacrydioides* was the species with the lowest mortality rate (17 %). Only 2 merchantable individuals of *P. totara* were measured in 1959 and none of them had died in the following 43 years. These values represent annual mean mortalities of 0.3-0.9 %.

Table 32. Mortality of merchantable podocarps over a period of 43 years in a 15 ha control block of a selective logging trial that were tagged and measured in 1959 and 2002

	1959		2002		mortality (43 years)		mortality yr^{-1}
species	***n***	***n* ha^{-1}**	***n***	***n* ha^{-1}**	***n***	**%**	**%**
Dacrycarpus dacrydioides	36	2.4	30	2.0	6	17	0.4
Dacrydium cupressinum	231	15.4	160	10.7	71	31	0.7
Podocarpus totara	2	0.1	2	0.1	0	0	0
Prumnopitys ferruginea	65	4.3	39	2.6	26	40	0.9
Prumnopitys taxifolia	41	2,7	29	1.9	12	29	0.7
total:	375	25	260	17.3	115	30	0.7

This decline of emergent podocarps was not related to particular diameter classes but affected the whole diameter range of all four species (Figure 56).

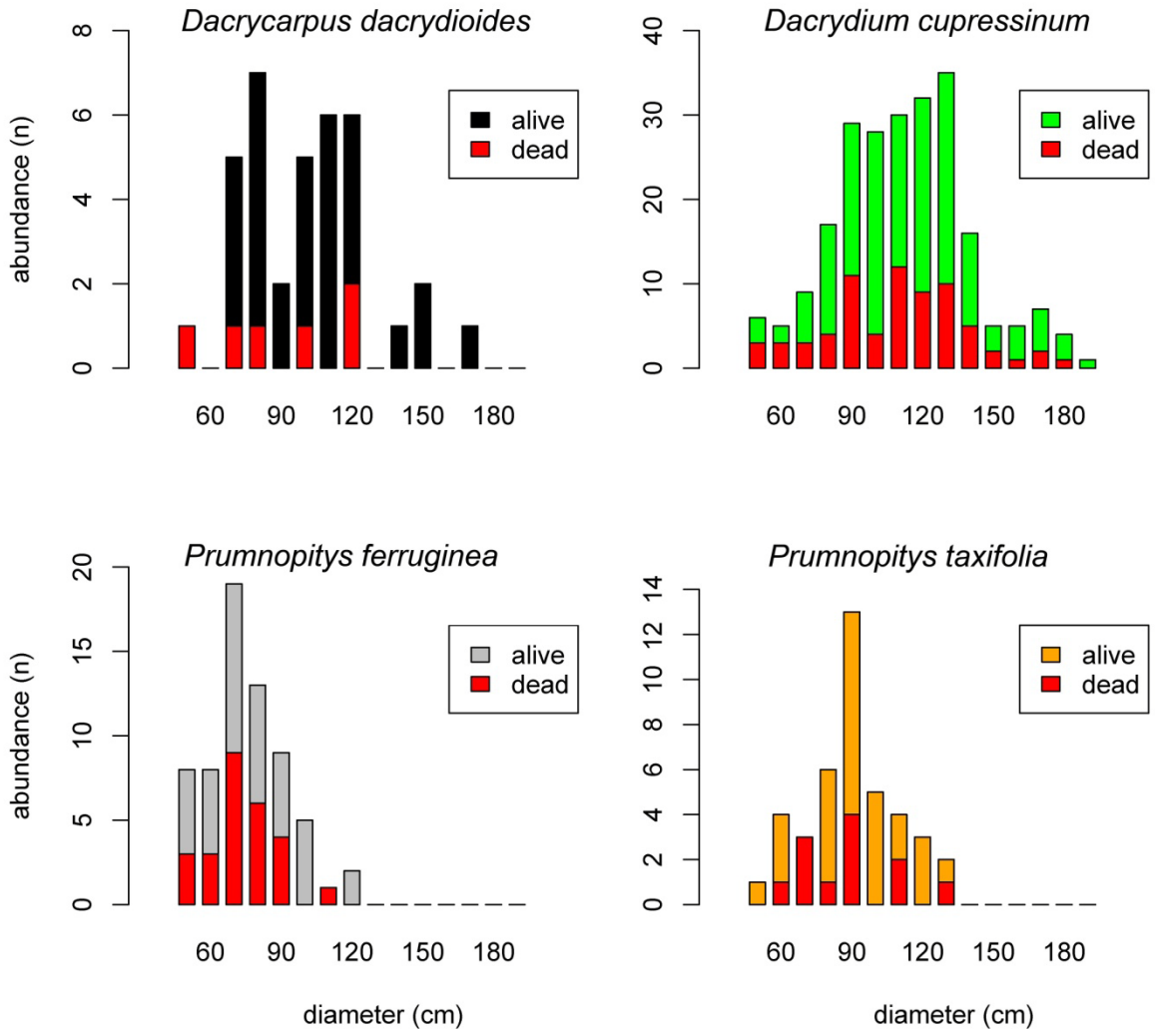

Figure 56. Absolute mortality of emergents of 4 different podocarp species in a 15 ha sampling block over a period of 43 years.

If the decline of emergent podocarps continues at the same rate it did in the period 1959-2002, no more emergent podocarps of the sampled class will tower above the forest at the study site by the year 2200 (Figure 57). The first species to disappear will be *P. ferruginea*, around the year 2060. *Dacrydium cupressinum* and *P. taxifolia* will follow around the year 2100 and trees of *D. dacrydioides* will be the last emergent podocarps to disappear around the year 2200.

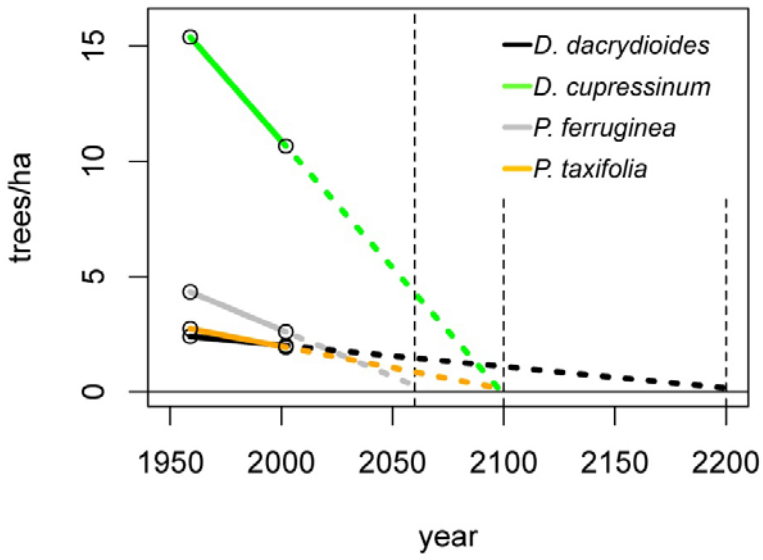

Figure 57. Simplified extrapolation of mortality of emergent trees of 4 different podocarp species between 1959 and 2002 (solid lines) and a simple prediction of their disappearance as emergents at the study site (dashed lines); *n* = 375.

3.3.11. Growth Cycle

The forest at the study site consists of an extremely heterogeneous mosaic of patches of different aged trees, representing different phases of the forest growth cycle (Table 33). The time span for each of those phases was estimated with the help of increment cores. Most gaps were created by the death of 1 or 2 large canopy trees and the gap phase was estimated to last for up to 50 years. But there were also gaps over 50 years old that were dominated by the tree fern *D. squarrosa* without any signs of canopy species establishment. Here the succession from the gap phase to the building phase seems to be arrested, as the tree ferns seem to replace themselves for decades until they are colonized by epiphytic seedlings of *W. racemosa*, *Pseudopanax arboreus*, *Raukaua edgerleyi* and *Griselinia littoralis*. Seedlings of those species find a suitable substrate for establishment in the interstices of slowly decaying frond bases on the caudex. From there, they grow into the crown of their hosts and send a primary root down to the ground. They slowly start to strangle the tree fern by developing horizontal branch roots, eventually killing the host (Dawson, 1988). With those angiosperms replacing tree ferns, other gymnosperm and angiosperm tree species become established directly in the soil, closing the gap that was occupied by tree ferns earlier. In this case, the gap phase might well last for over 100 years.

The building phase was estimated to take between 50 and 100 years but can take up to 200 years, depending on the level of disturbance and the species. The dimensions of building phases within a few plots indicate that larger disturbances must have occurred in the past. In the mature phase, trees are growing within the main canopy from 100-300 years of age while they reach heights of 20-30 m. At that stage height growth stagnates for most angiosperm species but continues for the podocarps. Once they passed this canopy, there is no more angiosperm competition for light.

The senescent phase in the forest depends on the tree species in focus and starts to appear at around 300 years of age for *B. tawa* but much later for the podocarps. Due to their longevity and depending on the species, podocarps can take several hundred years before they show signs of senescence. But with sounding of large trees not returning clear signals, no such tree was cored and age estimation had to be based on historic ring counts in felled trees.

Table 33. Growth phases, their age span and distribution (% of plots featuring the phase) within the podocarp-broadleaved forest at the study site with senescent phases for angiosperms (a) and podocarps (p)

Growth phase	Description	Time	Plots (%) covering the phase
Gap phase	Canopy disturbance is promoting regeneration	0 – 50 yrs	26
Building phase	A subcanopy is formed by regenerating tree species	50 – 100 yrs	66
Mature phase	Intact main canopy of 20-30 m height	100 – 300 yrs	100
Senescent phase (a)	Old, overmature senescent trees that are slowly dying	> 300 yrs	75
Senescent phase (p)	Old, overmature senescent trees that are slowly dying	> 500 yrs	88

The growth phase that occurred least often was the gap phase. Those gaps were mainly created by single tree death and occupied by tree ferns or seedlings and saplings of *B. tawa*. The building phase was spatially localized in smaller or larger gaps. The mature phase occurred in every plot. The senescent phase of angiosperms was always assigned to individual trees while the senescent phase of the podocarps was assigned to the whole cohort of emergent trees. The different growth phases were spatially of very limited extent and sampling plots could cover 4 phases (22 % of plots), 3 phases (47 % of plots) or 2 phases (31 % of plots), while plots with only one phase did not occur.

3.4. Discussion

3.4.1. Forest composition

A list of tree species occurring at the study site was prepared before sampling plots were established. Here, 8 gymnosperm species, 67 angiosperm species, 2 monocotyledonous tree species and 4 tree fern species were recorded. This means that only 30 % of the initially recorded species were sampled in plots. The main species missing were early successional angiosperms. Owing to the random sampling approach that was chosen to investigate the general forest composition, those tree species that were rare or appeared spatially clustered were less likely to be recorded. But even the list of the preliminary study was not complete in comparison to earlier full species lists compiled by Wilcox (1999) and Wallace, Leathwick, Williams, Simmons and Wardle (Leathwick, 1987). This is a common problem not only in botany but also in wildlife biology, and many publications deal with the problems of sampling species that occur infrequently in an ecosystem (Guisan et al., 2006; Meynard & Quinn, 2007; Thompson, 2004). To avoid this problem, forest ecologists in the tropics tend to use full inventories of forest blocks of up to 50 ha, where every tree species is measured and mapped (Condit et al., 2000). But as the objective of this study was not a full species inventory but a study of the general patterns and dynamics of podocarp-broadleaved forest and the regeneration success of podocarps in particular, the approach chosen was found to be suitable with all canopy tree species occurring in plots (see Appendix).

The frequencies and abundances of tree species illustrate the low light conditions in the forest. The species that are most shade-tolerant or shade-resistant showed the largest frequencies and abundances; light-demanding species were rare. The most frequent and abundant tree species in all diameter classes at the study site was the extremely shade-tolerant *B. tawa*, a late successional species that is often the dominant tree species in podocarp-broadleaved forest on the Volcanic Plateau in the Central North Island (Knowles & Beveridge, 1982; C. J. West, 1986). *Elaeocarpus dentatus* and *W. racemosa*, both found frequently throughout the forest in the subcanopy, also appear to be reasonably shade-tolerant or at least shade-resistant. Several authors suggest that they are shade-tolerant in

their early youth but require more light later in life (Bellingham & Richardson, 2006; M. C. Smale & P. N. Smale, 2003). Several of the other angiosperm tree species at the study site such as *M. ramiflorus* and *M. australis* are also known to be shade-tolerant or at least shade-resistant (Lusk & Jorgensen, 2013; Lusk et al., 2009; Lusk, Kaneko, Grierson, & Clearwater, 2013; Williams & Buxton, 1989).

The frequency and abundance of podocarps at the study site seem also to be related to their shade tolerance in the following order from most to least shade tolerance: *P. ferruginea* > *D. cupressinum* > *P. taxifolia* > *D. dacrydioides* > *P. totara*, an observation which is in line with findings of earlier studies (M. C. Smale, B. R. Burns, P. N. Smale, & P. T. Whaley, 1997). The shade-resistant species *P. ferruginea* and *D. cupressinum* were the only podocarps that occurred in reasonable numbers in smaller diameters, whereas more light-demanding *P. taxifolia, P. trichomanoides* and *D. dacrydioides* were rare. While the light conditions within the forest were regarded as the main reason for the abundance of species, soil conditions have also been found to play an important role in the occurrence of *D. dacrydioides* and *P. taxifolia* (Carswell et al., 2007; Coomes, Kunstler, Canham, & E. F. Wright, 2009; Dawson, 1988). In particular, *D. dacrydioides* was often found on wetter sites, an observation that has been confirmed in several other studies (Leathwick & Austin, 2001; Urlich et al., 2005). Data collected at the 8 additional sampling points showed that those sites were also stocked with *D. dacrydioides* in pole size classes 1-2. But even in those additional plots, no individuals of *P. taxifolia* were found in any diameter class < 70 cm.

The presence of very large *P. totara* and absence of this species in any other diameter class as well as sapling and seedling classes seems to indicate that these trees are old and might have established during an earlier successional stage. Under the current growth conditions they are not able to replace themselves any more (M. C. Smale et al., 1997). One other example of such an old tree is called Pouakani Tōtara, growing 6 km southeast of the study site and is the largest *P. totara* in New Zealand that survived the harvesting frenzy at Pureora (Figure 58). It is estimated to be over 1500 years old and represents the first cohort of podocarps that established on the Volcanic Plateau after the Taupo eruption (Burstall & Sale, 1984). However, there is no indication that the individuals found at the study site have a

similar age but their scarcity indicates nevertheless that they must have established under growth conditions that were very different to the ones found today in the forest.

Figure 58. Pouakani Tōtara, the largest *Podocarpus totara* in New Zealand

3.4.2. Regeneration

Seedlings and saplings of ***Beilschmiedia tawa*** were found in every sampling plot and their abundance supports the dominance of this species throughout the forest. This compares with findings of Smale (2008), who analysed *B. tawa* seedling data of 31 permanent 0.0081 ha plots in mature *B. tawa* dominated forest in the Otamatuna Management Area of Te Urewera National Park from 1997 and 2006. He divided the occurring seedlings in similar height classes to the ones used in the presented study (< 15 cm, 15-45 cm, 46-135 cm) and calculated densities between 1,006 and 1,394 seedlings ha^{-1} for height class 1, 387-413 seedlings ha^{-1} for height class 2 and 452 seedlings ha^{-1} for height class 3. The numbers in the present study obtained in podocarp-broadleaved forest were much higher in all height classes (class 1 = 6,354 seedlings ha^{-1}; class 2 = 1,910 seedling ha^{-1}; class 3 = 2,431 trees ha^{-1}; class 4 = 2,674 saplings ha^{-1} ; class 5 = 469 saplings ha^{-1}), with the total number of *B. tawa*

seedlings of height classes 1-3 in podocarp-broadleaved forest (10,695 seedlings ha^{-1}) being around 5 times higher than in *B. tawa*-dominated forest in Te Urewera (1,858-2,232 seedlings ha^{-1}). This is in line with findings in two 0.0384 ha transects at Pureora that were established in 1959 where *B. tawa* seedling densities for height classes 1-3 (6,432-25,104 seedlings ha^{-1}) and classes 4-5 (182-6,484 saplings ha^{-1}) were found to be much higher than in *B. tawa*-dominated forest at Te Urewera, even though they varied significantly (M. C. Smale, 2008). Densities for *B. tawa* saplings of classes 4-5 (3,143 seedlings ha^{-1}) calculated in the present study were around the mean of the numbers calculated by Smale (2008) for podocarp-broadleaved forest. But he found that numbers of seedlings at Te Urewera differed significantly between hillslope (1,429-1,714 seedlings ha^{-1}) and terrace (2,571-3,600 seedlings ha^{-1}), in particular for height class 1 (857-1,200 seedlings ha^{-1} vs. 1,943-2,914 seedlings ha^{-1}).

West (1995) carried out her PhD research in the North Block of Pureora Forest some 8 km west of the present study site, where she found even fewer seedlings of *B. tawa* with 341 seedlings ha^{-1} in height class A (0-15 cm), 246 seedlings ha^{-1} in height class B (15-30 cm) and 206 seedlings ha^{-1} in height class C (30-150 cm) as well as 2,472 saplings ha^{-1} in diameter class D (0-5 cm dbh). But her study site was in a forest with higher basal area, suggesting that seedlings have a negative correlation with the basal area in the forest. In addition, she observed survival rates of 76-95 % for seedlings and 98 % for saplings within a 3-year period. Unfortunately, no information regarding survival rates are available for seedlings at the present study site. However, the different frequencies and densities in the 24 seedling transects highlight the spatial variations within podocarp-broadleaved forest.

Some biotic factors that were suggested to influence the frequency and densities of *B. tawa* regeneration are browsing by introduced mammals such as deer (*Cervus elaphus*), possum (*Trichosurus vulpecula*), feral cattle (*Bos Taurus*) and goats (*Capra hircus*), decline of fruit-dispersing kereru, seed predation after seedfall and abiotic factors such as wind exposure, drought, snow and frost (M. C. Smale, 2008).

Seedlings of ***Dacrycarpus dacrydioides*** were abundant throughout the forest, occurring in height class 1 in 54 % of all plots, whereas emergent trees of that species were found only in 25 % of them. This species has an extremely high reproduction potential, producing as many as 4.5 million viable seeds per tree in a mast year (Beveridge, 1964). Such a mast year was observed in 2014 when innumerable native birds, mainly tui, kereru, bellbird and North Island kaka (*Nestor meridionalis septentrionalis*) were feeding in the crowns of emergent trees and the forest floor was covered by millions of ripe seeds. These seeds germinate readily after seedfall. But the numbers of seedlings declined from one height class to the next by the factor 10 while no saplings were found. This is in line with findings of Beveridge (1973) for Pureora and Duncan (1993) for Westland, where they found that even though *D. dacrydioides* seedlings established under a dense canopy, their mortality was high with most seedlings not living for more than 2 years due to the low light conditions in these forests. Ebbett & Ogden (1998) found in a study of seedling growth of 5 endemic tree species in New Zealand that *D. dacrydioides* showed the greatest height growth response to increasing light levels, underlining their light-demanding character. Their low abundance in any diameter class below 90 cm while occurring in relatively high numbers of 1,719 seedlings ha^{-1} in seedling height class 1 indicate that light-conditions for this species were not favourable for a long time. A reason might be that *D. dacrydioides* is able to produce numerous seeds that germinate readily and evenly, resulting in an abundant supply of regeneration (Beveridge, Bergin, & Pardy, 1985). But due to their demand for light, those seedlings do not seem to be able to survive for many years unless light conditions improve.

Seeds of ***Dacrydium cupressinum*** germinate in late spring or summer after seedfall but with numbers of around 200,000 seeds per tree, are not as numerous as *D. dacrydioides* (Beveridge, 1964). Seedlings and saplings were neither frequent nor abundant even though they occurred in every height class with a slow but steady decrease from seedling class 1 (434 seedlings ha^{-1}) to sapling class 5 (17 saplings ha^{-1}). The relative shade-resistance of this species has been related to the extreme slow growth of seedlings, with seedlings in the forest taking around 35 years to reach 1.4 m height (Ebbett & Ogden, 1998; James, 1998). But it seems that this growth performance is not assignable to the species' potential, with Ebbett & Ogden (1998) reporting a mean height growth of 18.3 cm y^{-1} under glasshouse

conditions. However, the low abundance in particular in the sapling classes at the study site do not seem to be sufficient to provide significant numbers of mature trees in the future without a change in light conditions (James, 1998).

Phyllocladus trichomanoides was the rarest of the podocarps and with no seedlings or saplings and only two larger trees observed, it seems to be out of place in this forest type.

Conditions for successful regeneration of ***Podocarpus totara*** seemed to have been extremely unfavourable for centuries with no seedling or saplings being found in any transect and the only adult trees having diameters > 150 cm. Even though old trees can have poor seed crops (Bergin, 2000), at least individual seedlings were expected to be found. This is remarkable as Bergin (2000) reports that *P. totara* generally produces seeds in abundance.

Prumnopitys ferruginea was the most frequent and abundant podocarp species in all seedling and sapling classes as well as diameter classes up to 90 cm, showing a steady supply of regeneration that is advancing from one height class to the next. This is of particular significance as this species produces only around 32,000 seeds per tree (Beveridge, 1964). In addition, seeds take between 3 and 4 years to germinate. But survival rates are high and show that this species can regenerate well under a dense canopy of angiosperms. It does not need canopy gaps for seedling establishment and advanced growth of saplings, an observation that is shared by Duncan (1993) in Westland and Beveridge (1983) in the Central North Island. This species is generally regarded as the most shade-tolerant podocarp (M. C. Smale et al., 1997), growing well in intermediate light conditions. But it was also found to respond well to increasing light levels, making it well adapted to small gap creation (Ebbett & Ogden, 1998).

Seedlings and saplings of ***Prumnopitys taxifolia*** were generally scarce but occurred in all height classes in almost equal numbers, even though they decreased significantly in sapling classes. But no trees with diameters between 5 and 84 cm were found. Ebbett & Ogden (1998), however, report *P. taxifolia* to be an ubiquitous species with a similar shade-tolerance to *D. cupressinum*, occurring under all light conditions. But the authors also relate

the occurrence of this species to soil nutrient levels. If that is the case, the absence of *P. taxifolia* in diameter classes below 80 cm but comparably high abundance in larger diameters could indicate that growth conditions have worsened since the current generation of emergent trees established.

The frequency and abundance of seedlings within the forest seems to be related to their ability to tolerate shade. Lusk and Jorgensen (2013) measured the growth of seedlings of 5 different species with heights from 50 to 100 cm and by interpolating the height growth of various trees under different light conditions, used plant compensation points to determine their light requirements. Here, they found that low-light mortality was higher for *D. cupressinum* than for *P. ferruginea*, suggesting that seedlings of *P. ferruginea* are more shade-tolerant than *D. cupressinum*. Even though seedlings of *D. dacrydioides* and *D. cupressinum* were reasonably abundant at the study site, pole or mature trees with diameters up to 80 cm were rare. And the low numbers of *P. taxifolia* seedlings did not seem to produce any successful advanced regeneration at all. It seems that even though these seedlings can persist in shade for some time, light conditions barely improve to an extent that would support advanced growth.

3.4.3. Vertical structure

The forest showed the typical 5-tier structure with emergent podocarps above a dense main canopy of *B. tawa*, a subcanopy of angiosperms with scattered podocarps, a shrub tier with tree ferns and smaller shade-tolerant tree species, and a ground layer dominated by ferns (P. Wardle, 1991). The heights of the different tiers were found to vary between plots and while some large-diameter podocarps were only 25 m tall, the main canopy was in that case even lower. The overall density of podocarps in the emergent tier was 25 trees ha^{-1} with diameters from 70-200 cm. But a lack of podocarps in diameter classes below 70 cm becomes apparent. While only scattered individuals of *P. ferruginea* were found in diameter classes from 30-50 cm, there were no other podocarps in those classes. All podocarps with diameters > 70 cm were emergent trees that tower above the forest. All other tiers were dominated by *B. tawa* which is abundant throughout all diameter, height and social classes. It seems to be impossible for the podocarps to penetrate the *B. tawa* dominated canopy as

no podocarps of more than 5 cm diameter were found in or under this canopy. A small number of *P. ferruginea*, *D. cupressinum* and *D. dacrydioides* with heights between 10 and 20 m and diameters between 15 and 30 cm were found to be codominant (class 3) and subdominant (class 4) trees clustered in older gaps of the main canopy. *Elaeocarpus dentatus* and K. excelsa were found in the main canopy as class 2 trees as well as in older gaps as class 3 and 4 trees. The tree ferns *D. squarrosa* and *C. smithii* were common features of the shrub layer.

Height modelling of 4 podocarp species illustrates a height gap, with trees of heights between 20 and 30 m missing in the forest. The height-diameter relationships of *D. dacrydioides* and *D. cupressinum* indicate that emergent trees do have a different relationship to the smaller diameter trees. This could be a result of the senescence of emergent trees, representing height loss due to crown dieback. None of the crowns appeared intact and it can be assumed that those trees were somewhat taller in the past. *P. ferruginea*, however, did not share this relationship. But as no trees in middle diameter classes could be measured and the number of measurements was generally small, these height models can be expected to be incomplete. *B. tawa* was the only species that showed a wide-ranging distribution of diameter and height measurements and dominated the subcanopy as well as the main canopy of the forest. Trees of *E. dentatus* were found mainly in the subcanopy but also scattered in the canopy where height growth seems to diminish considerably with increasing diameter. Heights and diameters of *E. hookerianus* and *N. lanceolata* were similar to those of the podocarps in the subcanopy. With the exception of *E. dentatus* and *K. excelsa*, all other tree species were generally absent from the main canopy. Only few large diameter *P. ferruginea* and *P. taxifolia* were found with heights that assign them to the main canopy. But in those cases the main canopy was lower and the podocarps were still emerging from it.

Analysis of the different social classes of trees showed that 35 % of the podocarps were codominant trees. That means even though these trees had heights that assigned them to the subcanopy, they in fact appeared in gaps and were not beneath the main canopy. The tree species most affected were *D. dacrydioides* (100 %), *D. cupressinum* (78 %), *P.*

trichomanoides (100 %) and *P. ferruginea* (46 %). But all measured angiosperms of *K. excelsa* and *N. lanceolata* were also found to be codominant trees without a covering main canopy. Subdominant trees which are actually growing in the subcanopy belonged mainly to the shade-tolerant podocarp species *P. ferruginea* (54 %) and only to a lesser extent to *D. cupressinum* (20%), *B. tawa* (26 %) and *E. dentatus* (11 %).

3.4.4. Age structure

The estimated age for trees represents the age at coring height at 30 cm above ground. This has to be taken into account when the total age of a tree is to be estimated. To reach that height, it was found earlier to take seedlings from 2 to 5 years after germination (Beveridge, 1973; Beveridge & van Dorsser, 1980). But as these values were not investigated in the present study, only age estimates in coring height are used. Sounding of trees showed that internal decay is a common feature in all emergent podocarps. In particular, the podocarps with larger diameters were often hollow, a common finding in emergent podocarps (Bergin, 2000; Hinds & Reid, 1957). But also *B. tawa* and *E. dentatus* of diameters larger than 50 cm were likely to contain internal rot according to results of sounding, either returning clear signs for decay or suspicious sound. The method proved to be a good field based measure for the detection of internal decay. As a result, no emergent podocarps were cored and only few angiosperms with diameters larger than 40 cm. But Smale et al. (1987) report an age range of 440 to 620 years for seven healthy emergent *D. cupressinum* that were aged based on ring counts at stumps in 1961 during a harvesting trial next to the study site. This indicates that the current emergent podocarp tier does not necessarily represent one even-aged cohort of senescent trees that established at the same time. But ocular age estimation in the field is prone to substantial error and those results are to be treated with caution.

In a similar podocarp-broadleaved forest north of Pureora forest on the Mamaku Plateau in the Central North Island, Smale et al. (1997) differentiated on the basis of increment cores emergent trees of two age ranges for emergent *D. cupressinum* (400-700 years and 800-1000 years) and for *P. taxifolia* (400-500 years and 800-900 years). However, as they

sampled only nine and three trees respectively, these age estimations do not necessarily represent the whole population of emergent podocarps.

Most of the emergent podocarps at the study site were affected by internal decay, making age estimation difficult. One solution to this problem might be to sound trees with internal decay at different heights and to core them at a height where sound timber can be expected. Even though this could mean that coring might be necessary in 5 m height or more, the estimated age at that height can be used as a starting point for total age estimation. By modelling the relationship between age and height, based on sound trees, the missing age for the bole section below the coring height of hollow trees can be estimated. Being able to age a sufficient number of emergent podocarps would enable the establishment of a stand history for these species to investigate if those emergents do reflect a whole cohort of trees or if they established independently from each other.

The majority of current codominant and subdominant podocarps as well as *E. dentatus,* were found to be within an age range of 60 to 100 years. Older age classes of *D. dacrydioides*, *D. cupressinum* and *P. trichomanoides* were not found except the senescent emergent podocarps that tower above the forest and a single 249 year old *D. cupressinum* with only 25.0 cm diameter. The majority of *P. ferruginea* (98 %) was between 57 and 147 years old and covered a wider age range than all other podocarps. The age distribution of sampled *E. dentatus* covered trees from 36 to 156 years, but the average age was 79 years. Due to larger diameter trees of that species being prone to internal decay, no such trees were cored. Therefore the cored trees are most likely to not cover the complete age span of *E. dentatus* in the forest with older age classes missing. Cored trees of *B. tawa*, though, occurred in an age range of 50 to 358 years. Taking into account that here larger diameter trees were also found to be affected by internal decay, the full life-span of this species can be expected to be much higher than the 200-300 years stated by Knowles & Beveridge (1982). This is confirmed by age estimates of West (1986), who cored *B. tawa* as old as 458 years. All age estimates, however, include an error as elaborated in Chapter 2 for *B. tawa* and also confirmed for *D. cupressinum* (G. H. Stewart & J. C. White, 1995) and *D. dacrydioides* (Duncan, 1989).

The small number of observations and the small age range of cored trees restricted the possibilities of statistical analysis. Only tree species with more than 30 observations were therefore selected for modelling.

Diameter/age relationship

The estimated age range of most podocarp species was quite narrow and covered barely 40 years, with diameters ranging from 9-35 cm. These trees reflect a cohort that established within a time frame of 40 years, with a mean age of 87 years. This was particularly apparent in *D. cupressinum*, where trees of 79-88 years (age span of 9 years) ranged in diameters from 9.1 to 35.2 cm. For a similar diameter range, a larger age range was observed for *P. ferruginea*, where 45 observations covered an age span of 100 years. Despite this large variation, a positive correlation was found between diameter and age with three models being compared in form of an AIC test (simple linear regression, polynomial regression, non-linear regression) with the polynomial model showing the lowest AIC. But considering the maximum life-span of this species, modelling of a period this short gives only a limited picture of this relationship. Owing to the small number of podocarps encountered at the study site, no further modelling was carried out in that respect.

The samples taken from *B. tawa* covered a diameter range from 12.8 to 66.2 cm with an age span from 47-358 years. Even though the largest trees at the study site could not be cored due to internal decay, 80 % of the encountered diameter range (up to 82.2 cm) was covered. Modelling showed a strong positive correlation between diameter and age, with a simple linear regression providing the best fitting model. The oldest tree without internal decay was 358 years old and had a diameter of 57.5 cm. This tree did not show any signs of senescence and it can be assumed that the life-span of 200-300 years given in literature (Knowles & Beveridge, 1982) is not representative for the forest at the study site. This observation was also made by West (1986) who found a diameter range from 11.2 to 107.6 cm for trees 49-458 years old. Trees with diameters < 10 cm are difficult to core and were therefore not included in this part of the study.

Even though samples of *E. dentatus* covered a diameter range of 11.6-42.6 cm, 80 % of the trees were between 60 and 100 years old, with a similar age range to the podocarps. But the diameter range within that age range was larger. While the relationship between both variables was significant, the variation in the relationship was very large and the best fit linear model explained only 14 % of it.

According to the modelling results for 100 year old trees, *E. dentatus* had the largest mean diameters (28.4 cm) while diameters of *P. ferruginea* (19.2 cm) and *B. tawa* (19.5 cm) were similar. This means that *E. dentatus* had the largest diameter growth of these three species, while it was similar for *P. ferruginea* and *B. tawa*.

The problem of a small sample size and diameter range in case of the podocarps, and a small age range in spite of a large diameter range in the case of *E. dentatus* and *D. cupressinum*, highlight the difficulties in examining the relationship of those variables, in particular when certain diameter and age classes are rare in the forest. Other factors such as inter- and intraspecific competition as well as site conditions can be expected to influence this relationship considerably.

3.4.5. Height growth

The relationship between height and age of trees was used as an indication for the mean annual height growth under the growth conditions at the study site. But the number of podocarps encountered in the forest was extremely low. In addition, most tree species covered only a short age range in combination with a large range of heights. *B. tawa* was the only exception, where 82 % of the species' height range was covered. A problem that occurred with *B. tawa* as well as *E. dentatus* was that larger trees showed signs of internal decay and could therefore not be sampled.

The annual mean height growth of species had large variations within social classes, even though trees of higher social classes were on average growing faster than trees of lower classes. For subdominant *B. tawa*, the mean height growth ranged from 6 cm yr^{-1} to 41 cm

yr^{-1}. While sharing the same social class, these were the slowest and fastest growing trees of all species and classes. Similar variations can be seen for *D. cupressinum* and *P. ferruginea*, where single individuals were found to be twice as old as the other class members. This means that even though trees had similar heights, their age could vary considerably. The age of subdominant *B. tawa* for example ranged from 47 years (height = 19.1 m) to 259 year (height = 21.1 m). It is therefore important that mean annual increments are treated with care if young trees and old trees are mixed in the analysis because the social class of a tree is not based on tree age or height but on its social status in relation to the forest canopy. On the other hand, trees of similar age were found to vary considerably in height. Sampled trees of *E. dentatus* clustered around the age range from 70 to 80 years with heights from 13.0 to 19.5 m, while trees < 60 years and > 109 were rare and predictions outside the main range are therefore prone to substantial error. This is also the case for *P. ferruginea*, where the age range from 60 to 100 years is well represented but observations above this range are rare and do not necessarily reflect the mean height growth of the species at that age.

The actual height of a tree is not necessarily evidence for overall slower growth. When growth conditions within the forest change, height growth of older suppressed trees and of faster growing younger trees can be released at the same time, giving them the opportunity to grow side by side in a recently formed gap.

The investigation of annual height growth of native trees in New Zealand is often restricted to seedlings and saplings as their height growth is considered to be of greater ecological significance than that of pole trees or mature trees (Ebbett & Ogden, 1998; Enright et al., 1993; Lusk et al., 2015; P. Wardle, 1963a). But the mean growth rates of 16-20 cm (μ = 18 cm) for *D. dacrydioides*, 8-27 cm (μ = 19 cm) for *D. cupressinum* and 10-24 cm (μ = 16 cm) for *P. ferruginea* calculated for pole trees at the study site are generally in line with those recorded for seedlings and sapling by Beveridge (1973). He found that longitudinal growth of podocarps is generally slow with 7 to 30 cm yr^{-1} with *D. dacrydioides* being the fastest growing species and *P. taxifolia* the slowest. In a growth trial under optimal nursery conditions, he found that *P. totara* was able to grow 50 cm yr^{-1} while *D. cupressinum* grew only 20 cm. In native forest canopy gaps of 10 m diameter, he found that *D. cupressinum*

seedlings showed a mean annual longitudinal increment of 18 cm within the first 7 years after planting (best 20% of seedlings). Another study that was carried out at the same site, calculated height increments based on repeated measurements of seedlings and saplings < 2.5 cm dbh for the period 1961-1983 (M. C. Smale & Kimberley, 1986). The increments of those smaller trees correspond well with the calculated values for dominated class 5 trees in the present study.

Comparing the mean annual height growth for trees < 100 years showed that *B. tawa* is the fastest growing species (24 cm yr^{-1}), followed by *E. dentatus* (23 cm yr^{-1}), D. cupressinum (19 cm yr^{-1}) and finally *P. ferruginea* (17 cm yr^{-1}). This is in line with the results of the comparison of modelled heights for 80 year old trees of *B. tawa*, *P. ferruginea* and *E. dentatus*. *Beilschmiedia tawa*'s dominance in the forest reflects its ability to grow under low light conditions.

But periods when height growth ceases as well as negative growth can alter the actual annual growth values of the different species considerably. Minimum and maximum growth of a tree can therefore be much lower or higher. Due to recent crown breakage for example, the height measurements of two *D. cupressinum* and one *P. trichomanoides* were not used for further analysis.

3.4.6. Diameter growth

The podocarps at the study site were found to overall be rather slow growing with a mean radial increment of 2.2 mm yr^{-1}. Growth rates of *D. cupressinum* (2.4 mm yr^{-1}) and *P. ferruginea* (2.1 mm yr^{-1}) were found to be higher than the North Island overall mean for those species which were 2.3 mm yr^{-1} and 1.5 mm yr^{-1} respectively (Hurst, Richardson, Wiser, & Allen, 2007) but lower for *D. dacrydioides* (2.4 mm yr^{-1}) in comparison to the North Island mean of 2.7 mm yr^{-1}. But the number of observations for the latter species was fairly small in both studies. In addition, only one mature podocarp each of the species *D. cupressinum* and *P. ferruginea* with diameters > 30 cm were cored in the present study. Smale & Beveridge (2007) who calculated the mean diameter increment for emergent podocarps at Pureora for the period 1961-2004 found mean growth rates of 1.8 mm yr^{-1} for

D. dacrydioides, 1.1 mm yr^{-1} for *D. cupressinum*, 1.0 mm yr^{-1} for *P. ferruginea* and 0.6 mm yr^{-1} for *P. taxifolia* yr^{-1}. These extremely low values in comparison to the diameter growth rates of social classes 2-5 calculated in the present study, seem to reflect senescence, decay and crown conditions of those emergent podocarps (M. C. Smale & Beveridge, 2007). Including them into the growth analysis of the present study would reduce the mean annual increment of those species significantly.

In an earlier study that was carried out at the study site, the periodic mean increment for different social classes of *D. cupressinum*, *P. ferruginea* and *B. tawa* was calculated for the period 1961-1983 (M. C. Smale & Kimberley, 1986). These values were calculated based on repeated diameter measurements of tagged trees in 10 subjectively placed circular plots and matched those calculated for 50 years from 1963-2013 presented in the present study and calculated on the basis of increment cores in particular for higher social classes.

The range of mean growth varied considerably between the different species and seems to correspond with their shade tolerance. Shade-resistant *P. ferruginea* (1.3-3.3 mm yr^{-1}) and *D. cupressinum* (1.0-4.4 mm yr^{-1}) showed the slowest growth, while the more light-demanding *D. dacrydioides* (2.1-3.0 mm yr^{-1}) and *P. trichomanoides* (2.5-3.1 mm yr^{-1}) had a minimum growth that was 2 times larger. The sample size of those two species, however, was very small and these results have to be treated with care. Comparing the maxima and minima of annual diameter growth of the different podocarp species showed that individuals of *D. cupressinum* had the largest (4.4 mm yr^{-1}) as well as the smallest mean annual growth (1.1 mm yr^{-1}).

E. dentatus (1.3-5.6 mm yr^{-1}, μ = 3.4 mm yr^{-1}) was overall the fastest growing species and *B. tawa* (0.8-5.2 mm yr^{-1}, μ = 1.9 mm yr^{-1}) the slowest growing. Still, both species were growing faster than the North Island overall means of 2.2 mm yr^{-1} for *E. dentatus* and 1.7 mm yr^{-1} for *B. tawa* (Hurst et al., 2007).

Smale et al. (2014) analysed 1722 *B. tawa* trees in the Central North Island and found that the average growth of a mature tree of dbh = 40 cm was 1.8 mm yr^{-1}. This was again smaller

than the mean increment calculated in this study for social class 2 and class 3 trees, even when comparing only the mean growth of class 2 trees over the past 50 years from 1964-2013, where the mean growth based on increment cores was 2.5 mm yr^{-1}.

This comparison of the mean diameter growth over those 50 years for social classes 3 and 4 shows that trees of higher dominance were generally faster growing individuals than trees of the same age but of lower dominance, which resulted in trees of different diameters having a similar age. But *B. tawa* trees of class 2 showed a slower mean diameter growth than class 3, indicating that older trees might have a smaller radial mean increment than younger trees. But the age range covered and the number of trees sampled was extremely low in particular in the case of the podocarps due to their general scarcity within the forest. Therefore the analysis was only carried out for *B. tawa* and *P. ferruginea*. Even though the analysis returned a significant relationship for *B. tawa*, the variance was extremely large and the explanatory value of the linear model used accordingly low. The problem of the large variance seems to be due to the fact that trees with similar age can vary significantly in diameter growth. But while in particular suppressed understorey trees were found to grow slower than dominant trees, including the social class as an explanatory variable did not improve the results significantly according to an AIC model comparison.

Within-tree growth variations

It was observed that all species showed a considerable range of annual increments not only between trees but also within trees. The variations in annual growth within trees was large with the widest rings being on average 8-16 times wider than the narrowest rings for podocarps and factor 13-15 for *E. dentatus*. Shade-tolerant *B. tawa* was found to grow extremely slow at times and the variations between the narrowest and the widest rings could differ by factors of 28-30. No significant correlation could be found between the social class of a tree and this variation in growth. This means that dominant trees as well as suppressed trees showed periods of slow growth as well as periods of fast growth.

The annual diameter increment ranged for *D. dacrydioides* from 0.14 to 7.97 mm (μ = 2.4 mm), *D. cupressinum* 0.18 to 10.53 mm (μ = 2.4 mm), *P. trichomanoides* 0.53 to 7.12 mm ($\bar{x}$ = 2.4 mm, *n* = 1), *P. ferruginea* 0.09 to 8.63 mm (μ = 2.1 mm), *B. tawa* 0.02 to 11.65 mm (μ = 0.19 mm) and *E. dentatus* 0.1 to 18.60 mm (μ = 1.9 mm), showing the potential of annual diameter increment for each species. *E. dentatus* was the fastest growing species, followed by *B. tawa* and *D. cupressinum*, while the other podocarp species showed slower maximum diameter increments. Richardson et al. (2009) calculated the median diameter increment of large trees (> 30 cm dbh) of six species based on repeated diameter measurements and received lower results for *B. tawa* (2.0 mm yr^{-1}) in comparison to the mean growth of 2.5 mm yr^{-1} in this study. But they selected their trees based on diameter and not based on social class. Interesting to note are the median diameter increments they calculated for tall trees (> 30 cm dbh) of *D. cupressinum* (3.3 mm yr^{-1}) and *P. ferruginea* (2.7 mm yr^{-1}). These diameters could not be covered in the presented study, but mean growth rates of social class 3 trees (dbh < 30cm) of *D. cupressinum* (3.1 mm yr^{-1}) and *P. ferruginea* (2.9 mm yr^{-1}) were extremely similar to those of the large trees of Richardson et al (2009).

Smale et al. (2014) found that neighbourhood competition has a major influence on the individual growth of a tree, which was confirmed by this study. But while the above authors report for mature canopy trees (dbh = 40 cm) growth rates of up to 2.4 mm yr^{-1} for low competition (40 m^2 ha^{-1}) and down to 1.3 mm yr^{-1} for high competition (120 m^2 ha^{-1}), this study found much higher individual growth rates between 4.10 and 8.54 mm yr^{-1} under low competition and growth rates as low as 0.04 to 0.36 mm yr^{-1} for high competition when focusing on the whole life-span of trees. A difference in site conditions may be the reason for this incongruity. But it is more likely that the exclusion of diameter increments for the time when trees were younger is causing this difference. However, the use of increment cores increases the accuracy of radial increment measurements on a stand basis in comparison to diameter tape measurements, particularly for slow growing trees, and there is no other way of estimating the historical annual radial increment of trees with such a slow growth in a non-destructive way (see Chapter 2). Here the exact same position of diameter measurements is paramount as even slight variations in measurement height can cause major errors in results for slow growing trees. In addition, problems due to buttresses,

different bark diameters over time and decay can cause over- or underestimation of annual growth (Richardson et al., 2009).

Stand life-history

Release and suppression were found to be a common feature of trees at the study side. While trees did generally not share phases of suppression and release with each other, there were also phases where multiple trees showed a growth release. One such phase of release was the period between 1936 and 1945, which affected in particular young seedlings and saplings of *E. dentatus*, *P. ferruginea* and *D. cupressinum*. This period coincides with New Zealand's most destructive cyclone of the 20th century that struck the North Island in early February 1936. On 31st January, a tropical storm from the Solomon Islands met a cold front north of New Zealand where it intensified its force and changed to an ex-tropical cyclone which crossed the North Island on 2nd February (MetService, 2011). Historical documents report that while heavy rain flooded most major rivers (the Mangakahia River in Northland rose by 19 m), washed away houses and caused severe landslips, the wind blew hundreds of thousands of trees down, either snapping or uprooting them. Trampers reported whirlwinds that twisted the crowns off trees. The storm had such a force that even train carriages were blown down their tracks and larger buildings such as churches were demolished. Most orchards in the affected areas were destroyed and crops of maize, wheat and oats flattened (MetService, 2011). Zotov et al. (1938) report that this storm completely levelled whole hillsides of forest in the Tararua Mountains south of Palmerston North within 2 hours from 10 a.m. to 12 p.m. when it gained its maximum force. Wind speeds of this storm were estimated to have been between 110 and 160 km/h (Thomson, 1936a). It affected trees of all diameter ranges and was reported to have uprooted countless emergent podocarps with large root plates up to 8 x 20 m diameter, leaving holes of 2 m depth. But they also report that *D. cupressinum* was the only podocarp species of which emergent trees were found to have survived the storm, even though they were badly damaged. They assigned this persistence to their special root architecture with surface laterals that exceed the radius of the crown and massive sinker roots (Cameron, 1963) as well as to the flexibility of their 'pendulous' branches (Zotov et al., 1938). The exact level of destruction at the study site

cannot be quantified, only the effect of the destruction in terms of growth response of surviving trees.

A general phase of suppression affecting several species began in 1950 and continued to increase with more and more trees being affected over time, indicating an increase of neighbourhood competition as a result of 1936 gaps closing in. This suppression accelerated steadily from 1995 onwards up to today. In particular, *D. cupressinum, P. ferruginea* and *E. dentatus* were found to be affected by this suppression. Seedlings and saplings of those species had shown a strong release in 1936 or got established in the aftermath. *B. tawa* on the other hand did not show any signs of increasing suppression.

3.4.7. The regeneration gap

The lack of middle-aged podocarps that this study identified is in line with what is called the 'regeneration gap of podocarps'. In the early 20th century, it was recognised that in mixed podocarp-broadleaved forest in New Zealand, overmature podocarps tower above a dense tier of angiosperms while saplings and young trees of those species are missing (Cockayne, 1928b). This lack of successful regeneration seemed to be a process that has been going on for several centuries and was regarded as a successional transition stage where mixed podocarp-broadleaved forest slowly passes over to broadleaved forest with an only minor presence of podocarps. This 'regeneration gap' was confirmed on a large scale during the National Forest Survey of New Zealand in 1955 (Masters et al., 1957) and it was feared that podocarps might be eliminated in the long run (Robbins, 1962). Trees as old as 50 years were observed to often not exceed 2.5 cm in dbh and similar slow growth rates of pole stands indicated that podocarps could not provide adequate future timber supplies.

Even though seedlings were found to be abundant on many sites, they were not able to survive and grow into larger size classes. One of the reasons for this failure to regenerate as well as the slow growth was in the past thought to be related to climatic changes. Holloway (1954) assumed that this climatic change from warmer and more humid conditions to cooler and drier ones must have occurred between the 11th and 14th century as the overmature and

senescent podocarps that are found today seem to be the last successful cohort and is believed to be between 500 and 800 years old. This theory was supported by Bathgate (1987), who analyzed 327 stem discs of *D. cupressinum*, reflecting this species' growth in the past 700-800 years. All trees showed a slow diameter growth between the 17th and 18th century that has since increased again. Other evidence for climatic change being the cause for failure of regeneration was seen in the lack of re-established podocarp forests after Maori fires 400-500 years ago. Instead of forests, xerophytic tussock grasslands now cover areas previously stocked with podocarp forest (Holloway, 1954a).

Wardle (1963) related the regeneration gap mainly to changes in the water regime, beginning in c. AD 1300 and having its climax in around AD 1800, causing podocarps to regenerate successfully only on the coolest and moistest sites. He agreed with Masters et al. (1957) that seedling growth is the most critical phase in regeneration where he related the lack of seedling survival to competition with ferns that reduce the available light in the understorey. Sites with better light conditions and shallow impoverished soils such as upper slopes or ridges were found to support much better seedling growth even though these sites are drier than gullies. An explanation for this regeneration success was attributed to the fast growth of seedlings and their roots in better light conditions, enabling them to exploit available soil moisture better in times of water stress (P. Wardle, 1963b).

But in lowland podocarp-broadleaved forest in the Central North Island, Beveridge (1973) found that even on sites with little fern competition, seedlings of *D. cupressinum*, *D. dacrydioides* and *P. ferruginea* take 20-50 years to reach 1-2 m in height. At this stage, growth stagnates until the canopy is opened up. However, light competition with tree ferns and shading angiosperms often prohibit seedling survival under natural conditions (Beveridge, 1973).

In the 1960s, the focus shifted from community composition to population dynamics, in particular different life-cycle strategies as proposed in the *r*/*K*-selection theory (MacArthur & E. O. Wilson, 1967), where some species follow the strategy of rapid population growth in open environments while others are more persistent and require more stable conditions for

reproduction. Following this approach, localized regeneration gaps were only reflecting demographic phenomena that are localised in space and time (Ogden, 1985). The age structure of podocarps in podocarp-broadleaved forest with the absence of several middle-age classes was believed to show that these trees just wait (if required, even for centuries) until conditions for their regeneration become more favourable again.

Lusk and Ogden (1992) found in podocarp-broadleaved forest near Horopito, Tongariro National Park, that the main age class of podocarps did not establish as a result of a cataclysmic disturbance but through progressive mortality of the overstorey. Due to the rapid disintegration of a whole cohort of podocarps and a subsequent canopy collapse, a new generation of podocarps, in particular *D. cupressinum* and *P. taxifolia* got established.

The low frequency of podocarps, however, is also observed for most of the smaller angiosperm tree species, in particular *Carpodetus serratus*, *M. australis*, *Pennantia corymbosa*, *P. eugenioides* and *P. arboreus*. These species are known to be light-demanding early successional trees, a feature that is also attributed to the podocarps. The examined disturbance history at the study site and the growth response of seedlings and saplings in relation to catastrophic disturbances support the theory of Beveridge (1973), where seedlings and saplings wait in the understorey for changing light conditions. When growth conditions improve, these trees can benefit from their well established root system. In addition, their already achieved height is an advantage in competition with newly establishing trees.

3.4.8. Mortality of emergent podocarps

The mortality rate of sampled emergent podocarps over the period of 43 years from 1959 to 2002 was 30 %. Here, *P. ferruginea* showed with 40 % (0.9 % yr^{-1}) the highest mortality followed by *D. cupressinum* (31 %, 0.7 % yr^{-1}), *P. taxifolia* (29 %, 0.7 % yr^{-1}) and *D. dacrydioides* (17 %, 0.4 % yr^{-1}). This annual mortality rate of 0.3-0.9 % yr^{-1} affected all diameter classes. As only merchantable podocarps were sampled in 1959, all cull trees with major timber defects were left out of this calculation. But as these trees were also mapped

in 1959 and most have died since, the absolute mortality since 1959 is higher than the above results imply.

Results of a similar analysis at the study site published earlier showed higher mortalities for *P. ferruginea* (1.0 % yr^{-1}), the same for *D. cupressinum* (0.7 % yr^{-1}) and lower for *P. taxifolia* (0.5 % yr^{-1}) and *D. dacrydioides* (0.2 % yr^{-1}) (M. C. Smale & Beveridge, 2007). In addition, these authors compared the mortality between two periods from 1961 to 1980 and from 1980 to 2004. According to those results, the mortality increased for *D. cupressinum* from 0.6 to 0.8 % yr^{-1} and *P. ferruginea* from 0.9 to 1.1 % yr^{-1} and decreased for *P. taxifolia* from 0.5 to 0.4 % yr^{-1} and *D. dacrydioides* from 0.3 to 0.2 % yr^{-1} resulting in an overall increase from 0.6 to 0.7 % yr^{-1}.

The prediction of the disappearance of senescent emergent trees of *P. ferruginea* by the year 2060, *D. cupressinum* and *P. taxifolia* by the year 2100 and *D. dacrydioides* by the year 2200 (Figure 57) is an oversimplified approach, as there is no indication that the relationship between time and mortality is linear and will continue the same way it did since 1959. However, the comparison of the mortalities of the two periods seems to indicate that the above prediction could even be conservative for *P. ferruginea* and *D. cupressinum*, if the observed trend continues. But no annual mortality values are given for each of those 43 years and those dates are to be treated as indicative only. On the other hand, catastrophic events such as the 1936 cyclone, even though they enhance growth releases, are a factor that increases the disappearance of emergent podocarps.

All emergent podocarps showed typical signs of advanced senescence with crowns dying back and foliage becoming sparse. And with all diameter classes affected in the same way, there is indication that they do represent a cohort of trees that established approximately at the same time. But only tree ring analysis of emergent trees as proposed above could answer this question. Whether or not those trees represent a single cohort or rather several cohorts, there is considerable indication that the extinction of a emergent podocarps is under way and will be completed in the foreseeable future (M. C. Smale, Beveridge, & Herbert, 1998).

Smale & Beveridge (2007) analysed the mode of death for 135 trees of the species *D. cupressinum* (*n* = 93), *P. ferruginea* (*n* = 31) and *P. taxifolia* (*n* = 31) at Pureora and found that standing death (40 %) was the most common mode of death, followed by uprooting (30 %) and snapping (30 %).

This trend of podocarp decline, however, does not seem to be restricted to emergent trees. Smale et al. (2016) analysed density and mortality data of 13 plots of 210 x 20 m (0.42 ha) that were established between 1957 and 1962 around Lake Taupo. For the Pouakani Block at Pureora, they report that podocarps with dbh > 30 cm underwent an annual decline between 0.18 and 0.30 trees ha^{-1} accounting for a basal area of 0.02 to 0.37 m^2 ha^{-1} yr^{-1} for a 40 year period, while at the same time angiosperms increased annually by 0.6 to 0.7 trees ha^{-1}. Based on those results they calculated the overall mortality rates for trees of major species with dbh > 30 cm and found that the annual mortality was the highest for *Podocarpus* spp. with 1.96 % (recruitment rate 0.2 %, net recruitment -1.76 %). *P. taxifolia* had an annual mortality rate of 0.7 % (recruitment rate 0.13 %, net recruitment -0.57 %), *D. cupressinum* a rate of 0.29 % (recruitment rate 0.1 %, net recruitment -0.19 %) and *P. ferruginea* a rate of 0.43 % (recruitment rate 0.53 %, net recruitment 0.10 %). The angiosperms *B. tawa* (annual mortality rate of 0.40 %, recruitment rate 0.87 %, net recruitment 0.47 %) and *E. dentatus* (annual mortality rate of 0.92 %, recruitment rate 1.68 %, net recruitment 0.76 %) on the other hand showed a strong increase in density. This means that light-demanding podocarp species *P. totara* and *P. taxifolia* were showed the largest decline, while shade-resistant *P. ferruginea* was the only podocarp species where the recruitment rate exceeded the mortality rate slightly. Mortality was found to have increased significantly from the 1960-83 period to the 1983-2000 period and seems to be in line with the increase of trees that undergo a growth suppression in this study. Smale et al. (2016) presume that this increase in mortality is a result of a whole cohort of more or less same aged emergent podocarps reaching its normal longevity of 500-700 years for *P. taxifolia*, 400-600 years for *D. cupressinum* and 600-650 years for *P. totara* and *P. ferruginea.* Richardson et al. (2009) who analysed the mortality of large trees (> 30 cm dbh) of 6 tree species from 28 plots that were established between 1958 and 1962 in old-growth forest across the Central North Island found annual mortality rates for *B. tawa* (0.60 %), *W.*

racemosa (2.21 %), *D. cupressinum* (0.16 %) and *P. ferruginea* (0.42 %) that were much higher in case of the angiosperms and much lower for the podocarps than the results provided by Smale et al (2016). Their values were much lower than the annual mortalities for *D. cupressinum* (0.7 %) and *P. ferruginea* (0.9 %) observed in this study, which represents the mortality rates of a senescent cohort of podocarps.

3.4.9. Growth cycle

The pattern of 2-3 growth phases co-existing within 40 m diameter plots shows the patchiness of the podocarp-broadleaved forest at the study site. This mosaic of different aged trees indicates gap-phase regeneration, with either progressive single-tree death or small-scale windthrow being the main system of canopy recruitment in this forest type (Martin & Ogden, 2006; Ogden, Fordham, Pilkington, & Serra, 1991; Veblen, 1992). Similar observations were made by Smale et al. (1997) in podocarp-broadleaved forest on the Mamaku Plateau in the Central North Island. This forest is also dominated by a main canopy of *B. tawa* and in addition *W. racemosa*, roofed by emergent podocarps *D. cupressinum* and *P. taxifolia*. On Mt Pureora, south of the present study site, podocarp-broadleaved forest with emergent *Podocarpus laetus* over *W. racemosa* and *Quintinia acutifolia* has similar growth cycle patterns (M. C. Smale & Kimberley, 1993). But there, the regeneration cycle of overstorey species contains a pattern where gaps are first invaded by tree ferns that are later colonized by early successional epiphytic broadleaved species which in turn facilitate the establishment on late successional overstorey species. This regeneration cycle was also observed to a lesser extend at the present study site in gaps that were colonized by *D. squarrosa* (Beveridge, 1973).

Progressive single-tree death can influence the duration of a gap phase significantly. It is even possible that no distinct gap phase occurs when regenerating shade-tolerant tree species slowly grow into a disintegrating crown of a senescent tree. Slow disintegration of single senescent podocarps does not create canopy gaps. If a created gap is small, it is also possible that it is closed before regeneration could benefit from its creation. Such is the case of toppling standing dead podocarps, where created gaps are often too small for

regeneration to establish. Those gaps are closed by surrounding trees before even already established regeneration can benefit from gap creation.

The small scale of disturbances created by single tree death at the study site does not seem to favour podocarps (Figure 59). Lusk et al. (2015) and Lusk and Jorgensen (2013) found that even though seedlings and saplings of most podocarp species are shade-resistant, there is a trade-off between shade tolerance and growth. While seedlings of these species can remain in low-light conditions for years, their ability to respond to increasing light levels is limited in comparison to light-demanding angiosperm tree species (Bond, 1989). As a result, small canopy openings are colonized by fast growing angiosperms such as *E. dentatus* rather than by podocarps.

Figure 59. Windthrow of senescent emergent podocarps does not create significant canopy disturbance

The shade-resistance of seedlings of podocarp species *D. cupressinum* and *P. ferruginea* (Lusk et al., 2009, 2013) gives them an advantage over light-demanding angiosperms when larger gaps are created. As they can establish and survive in the understorey for many years, they are already present as seedlings or saplings when a larger canopy disturbance occurs, as in the case of the 1936 storm. Those podocarps were already established and able to benefit from the change in the light environment as seen in the increase of growth releases around that time. Similar observations of successful disturbance induced regeneration of podocarps were made in Westland (Duncan, 1993; G. H. Stewart, 2002; G. H. Stewart et al., 1998; Urlich et al., 2005; Wells, Duncan, & G. H. Stewart, 2001; Wells, G. H. Stewart, & Duncan, 1998) and in the North Island (Martin & Ogden, 2006).

Large windthrow events are periodic features in New Zealand (Martin & Ogden, 2006). Their positive effect on podocarp regeneration, in particular through the destruction of a dense angiosperm canopy, was first described by Hutchinson (1928), supported by Roche (1929) and Thomson (1936b). The catastrophic cyclone of 1936 enhanced the establishment and growth of podocarp seedlings and saplings as well as the light-demanding angiosperm *E. dentatus*. This process is described in the temporal stand replacement or 'lozenge' model in *Agathis australis* forest, where substantial gap creation on a large scale releases a cohort of regeneration of the emergent conifer *A. australis* that subsequently replaces a cohort of senescent emergent trees (Ogden, 1985; Ogden & G. H. Stewart, 1995).

But the lack of middle diameter classes of podocarps indicates that those large disturbances are not common in podocarp-broadleaved forest at the study site. In addition, the extremely low densities of podocarps in 2013 and the suppression of growth they are undergoing since 1995 lead to the assumption, that the disturbance at the study site was not severe enough to promote the replacement of the emergent tier of senescent podocarps. This is particularly the case for *D. dacrydioides*, *P. trichomanoides*, *P. totara* and *P. taxifolia.* According to the densities and frequencies of podocarps encountered in this study, it seems likely that they will not play any major role at the study site in the foreseeable future.

3.5. Conclusion

The forest at the study site appears to be in transition from mixed podocarp-broadleaved forest to an angiosperm forest with only insignificant numbers of podocarps. The present population of emergent podocarps is declining steadily and they are likely to disappear in the foreseeable future. *Prumnopitys ferruginea* is, due to its shade-tolerance, the only species that is able to advance into higher diameter classes under a dense canopy of *B. tawa*. Even though seedlings of *D. dacrydioides*, *D. cupressinum* and *P. taxifolia* occur throughout the forest, these species are very rare in diameter classes between 2.5 and 90 cm, illustrating the regeneration gap of gymnosperms that is evident in many New Zealand forests (M. C. Smale & P. N. Smale, 2003; G. H. Stewart & Rose, 1989; Veblen & G. H. Stewart, 1982; P. Wardle, 1963b). Some subcanopy trees of *D. cupressinum* and *D. dacrydioides* were found in large canopy gaps that were formed during a catastrophic cyclone in 1936. At the time of the cyclone, those trees were seedlings and saplings and the growth release they showed after that event indicate that they required the higher light levels for advanced growth. The cyclone did, however, not stimulate recruitment of *P. totara* and *P. taxifolia* and even larger disturbances might be necessary to change their status in the forest.

Cohorts of emergent podocarps can persist in the forest for centuries until growth conditions for their replacement improve as a result of large-scale disturbances (M. C. Smale et al., 1998; Veblen, González, G. H. Stewart, Kitzberger, & Brunet, 2016; Wells et al., 2001). Similar observations have been made for other long-living emergent gymnosperms such as *Libocedrus bidwillii* (Ogden et al., 2005; Veblen & G. H. Stewart, 1982). But the scarcity of such large disturbances is evident in the small-scale patchy gap-phase regeneration in the forest, and can be regarded as the reason for the regeneration gap of podocarps here. Without large disturbances, the podocarps will slowly disappear from this forest type. *Dacrydium cupressinum* will linger on as a rare tree species while *P. ferruginea*, due to its shade resistance, will persist as a subordinate tree species despite the *B. tawa* dominance. Only few individuals of podocarps will be able to advance above the main canopy as emergent trees and the current podocarp-broadleaved forest will eventually become an

angiosperm forest dominated by *B. tawa* with only a very minor component of podocarps until catastrophic disturbances change growth conditions for them significantly.

Chapter 4

Regeneration success in central North Island mixed podocarp-broadleaved forest – the positive impact of large disturbance

4.1. Introduction

Forests are dynamic ecosystems that are constantly changing. Major drivers of significant ecosystem change are environmental disturbances of varying degrees (Pickett & P. S. White, 1985). Depending on their magnitude, they can affect whole landscapes (e.g., volcanic eruption (McKelvey, 1952; C. J. N. Wilson, 1985; C. J. N. Wilson & G. P. L. Walker, 1985), earthquakes (Wells et al., 2001), fire (Ogden, Basher, & McGlone, 1998), flood (Duncan, 1993)) or have a rather local impact (e.g. wind (J. A. Adams & Norton, 1991; Hosking & Hutcheson, 1998), insects and pests (Allen & W. G. Lee, 2006), frost (Knowles & Beveridge, 1982), drought (Grant, 1984)). Disturbances are mainly short-time events that happen over hours or days, sometimes weeks. While some are single events (volcanic eruption, earthquakes), others are common features of the environment (wind, frost) and can overlap in space and time or succeed each other.

Large-scale disturbances can set natural succession back to the beginning where all vegetation is wiped out, as in the case of volcanic eruptions. These bare sites have to be re-colonized by pioneer plant species with a subsequent succession of tree species, and can result in dense relatively even-aged forests of pioneer tree species (Baumgart & Healy, 1953; McKelvey, 1952). Far more often, however, are smaller disturbances that affect only certain species or groups of individuals and trigger secondary succession (D. C. West et al., 1981; H. D. Wilson, 1994).

All these disturbances change the forest ecosystem not only physically by damaging or destroying individuals but also by changing the growing conditions for the remaining trees and the interactions among trees (D. R. Foster, Knight, & J. F. Franklin, 1998).

4.1.1. Natural disturbances and silviculture

Disturbances in forest ecosystems are not always of naturogenic nature. In pre-European New Zealand, fire was often used for agricultural land clearance and hunting, with large areas of forest burnt (McWethy et al., 2009; Ogden et al., 1998; Ogden, Deng, Boswijk, & Sandiford, 2003; Perry, Wilmshurst, McGlone, McWethy, et al., 2012). On the other hand, felling trees for building, cooking or transport induced smaller disturbances (Cameron, 1964; McGlone, 1983b). The arrival of Europeans extended the use of timber to an industrial level with high-grading of forests (Figure 60) being the conventional way of exploitation (M. Roche, 1990). Here, all merchantable trees in a forest were harvested and logging slash as well as all remaining trees were subsequently burnt on site. In the 1950s, less destructive methods of forest management were investigated to sustain the yield. Holloway (1954) proposed strip felling of sub-mature and early mature *Dacrydium cupressinum* forests in Westland, while Beveridge (1975) established selective harvesting trials in mixed podocarp-broadleaved forest in the Central North Island by harvesting only a certain percentage of merchantable trees and maintaining the structure of the forest. To minimize forest disturbance during timber extraction, specialized heavy-lift helicopters such as the Russian Mil Mi-8 MTV with a lifting capacity of 5 tonnes played for some years a minor role in New Zealand (James & Norton, 2002). But costs were too high to make harvesting profitable and Heli Harvest, the country's largest heavy helicopter harvesting company ceased operation in September 2016.

The different silvicultural methods are management-induced disturbances that can alter the structure and composition of forests dramatically. In particular, the size of the disturbance has an important influence on light availability, soil conditions and regeneration as well as growth and survival of residual trees (C. D. Oliver, 1981). Understanding the impact of disturbances in forest ecosystems is the most important task for ecological silviculture (Benecke, 1996; Berry et al., 2008; R. J. Mitchell, Palik, & Hunter, 2002; Seymour & Hunter, 1999) that recognises that every tree species has its own growth requirements and its own adaptive strategies to respond to such disturbances.

Figure 60. Massive destruction during high-grading in Pureora Forest, Central North Island using a Caterpillar RD8 Diesel tractor with Hyster crawler logging arch (New Zealand Herald, 1953)

4.1.2. Focus of this study

An analysis of the structure of old-growth podocarp-broadleaved forest at Pureora disclosed the 'regeneration gap' of podocarps (Chapter 3). Even though seedlings and saplings of most podocarp species are present and even abundant, poles and mature trees are extremely rare despite abundant emergent trees of those species, indicating that growth conditions have been unfavourable for younger trees over the past centuries. Successfully established codominant podocarps were mainly found in larger gaps that were created by a catastrophic cyclone in 1936. In this chapter the relationship between canopy disturbance and tree species regeneration will be elaborated.

The following questions will be addressed:

1. **Does selective harvesting mimic the natural disturbance regime in podocarp-broadleaved forest?**

2. **What are the long-term effects of harvesting gap size on species composition in podocarp-broadleaved forest?**

3. **What is the impact of different scale canopy disturbances on the diameter increment rates of trees in gaps?**

4. **What canopy disturbance regime do podocarps require for successful recruitment and subsequent growth?**

For this purpose, the effects of disturbances of different scales are investigated 52 years after selective harvesting and 56 years after high-grading, and compared to natural disturbances in old-growth forest. Selective harvesting in this context refers to harvesting of small groups of emergent podocarps, whereas high-grading means harvesting of all merchantable trees. The data were collected from 2011-2014 and were analysed in 2015.

In addition, a harvesting inventory of the high-graded blocks was carried out in order to provide information about the abundance and distribution of emergent podocarps at this site. This was assumed to be an important indicator for the pre-harvesting emergent podocarp component in these blocks and was used to compare them with the selectively harvested forest and the old-growth forest.

Height increment is an important driver of inter- and intra-specific competition success. The faster a tree grows, the more likely it is to dominate neighbouring trees in their competition for light. But historic height increments are extremely difficult to measure in a non-destructive way. On the other hand, the social class of a tree is a measure of its crown competition status and was found to influence its diameter growth (Chapter 3). Therefore, diameter increments were used as a surrogate measure for the competition success of trees.

4.2. Methods

4.2.1. Study site

Around 100 ha of old-growth forest in the Māori blocks were high-graded in 1956/58 (Figure 3). Aerial photographs taken in 1950 show that this high-graded part contained old-growth podocarp-broadleaved forest with scattered emergent podocarps of the species *Dacrydium cupressinum, Dacrycarpus dacrydioides, Podocarpus totara, Prumnopitys ferruginea* and *Prumnopitys taxifolia* over a dense canopy of the angiosperm tree species *Beilschmiedia tawa*. After high-grading, almost no mature podocarps remained. Logging was uncontrolled and damage to the residual trees condoned as conversion to plantation with exotic tree species was envisaged (A.E. Beveridge pers. comm., 6. June 2012). However, the site was never replanted but left untouched ever since.

It appears that the level of destruction of the podocarp-broadleaved forest depended on the frequency of podocarps (Figure 61). While some parts of the forest were clearfelled, parts without any mature podocarps remained largely undamaged. Felling damage to residual trees was likely to be severe and much of the established regeneration will have been destroyed. This way, gaps of various sizes were created. The term ‘gap’ refers in this study to an opening in the canopy that extends at least down to the seedling tier of a forest and is confined by the vertical projection of the gap edges (Brokaw, 1982).

Harvesting damage was expected to not be restricted to plants. Hauling of trees alters the soil environment in the surface horizon through soil compaction and soil exposure (Reisinger, Simmons, & Pope, 1988) and new soil surfaces are created. Seeds of various plant species will have been unintentionally distributed by skidding along trails (Beveridge, 1973). But as this study is focusing on the effect of canopy openings on tree regeneration and subsequent growth, sampling plots that showed obvious signs of harvesting-induced major soil disturbance were excluded.

Figure 61. Different levels of forest disturbance are visible 5 years after high-grading in the two Māori blocks in 1956/58 (Ortho Photography: NZ Aerial Mapping, 1963)

While the two Māori blocks were harvested by uncontrolled logging, the selective harvesting trial that was established by the Forest Research Institute (FRI) in 1957 in the forest west of the Māori land had the objective of investigating prospects for sustainable yield management of podocarp-broadleaved forest. It was planned to harvest only 30 % of the merchantable timber and to cause minimal disturbance to the forest structure (Beveridge & Herbert, 1978). Therefore, three adjacent blocks of 15 ha each were demarcated and all merchantable podocarps were cruised and mapped. In addition, all unmerchantable cull trees were also mapped. Block A was a control block without any harvesting, while in block B podocarps in the centre of groups and in block C podocarps at the margins of podocarp groups were harvested in 1961 (Beveridge, 1975). These blocks are referred to as 'FRI blocks' in this thesis. The amount of cruised and harvested timber is shown in Table 34.

Table 34. Numbers of cruised and harvested trees in the three blocks of the 1961 FRI selective harvesting trial

	A-block	B-block			C-block		
	cruised	cruised	harvested		cruised	harvested	
Gymnosperms	*n*	*n*	*n*	%	*n*	*n*	%
Dacrycarpus dacrydioides	36	25	17	68	2	1	50
Dacrydium cupressinum	231	290	89	31	235	61	26
Phyllocladus trichomanoides	-	-	-	-	6	0	0
Podocarpus totara	2	-	-	-	1	-	0
Prumnopitys ferruginea	64	50	12	24	61	20	33
Prumnopitys taxifolia	42	25	9	36	13	6	46
total:	**375**	**390**	**127**	**33**	**318**	**88**	**28**
Angiosperms							
Beilschmiedia tawa	168	83	34	41	148	50	34
Elaeocarpus dentatus	25	8	3	38	19	5	26
Knightia excelsa	-	-	-	-	3	1	33
total:	**193**	**91**	**37**	**41**	**170**	**56**	**33**

The selective harvesting tried to remove the most senescent and unstable podocarps with open or damaged crowns. Healthy trees were to be retained in order to support the forest structure. The felling direction was marked for every tree with the aim of minimizing felling damage to residual trees and by using existing gaps. Existing regeneration of podocarps was to be spared from destruction. As the trial tried to mimic the size of natural disturbances, only small groups of 2-5 trees were harvested, creating gaps not larger than 0.1 ha. For groups of *B. tawa*, the recommended harvesting gaps size was 10-20 m in diameter. Cull trees were not to be felled due to their ecological values as habitat and seeding potential. Demarcation of skidder trails was used to minimize hauling damage to soil and residual trees (Beveridge & Herbert, 1978). The use of Caterpillar RD8 tractor haulers and Hyster crawler logging arches with caterpillar tracks enabled the hauler crews to manoeuvre large logs along narrow skidder trails in dense forest without causing significant damage to the residual forest (Figure 62).

The two high-graded Māori blocks as well as the FRI blocks offer the opportunity to compare the effect of canopy disturbances of different magnitudes on forest structure and tree species regeneration in podocarp-broadleaved forest five decades after gap formation. In addition, the A-block of the FRI trial as well as the surrounding old-growth forest serve as a comparison of natural disturbances and human-induced disturbances.

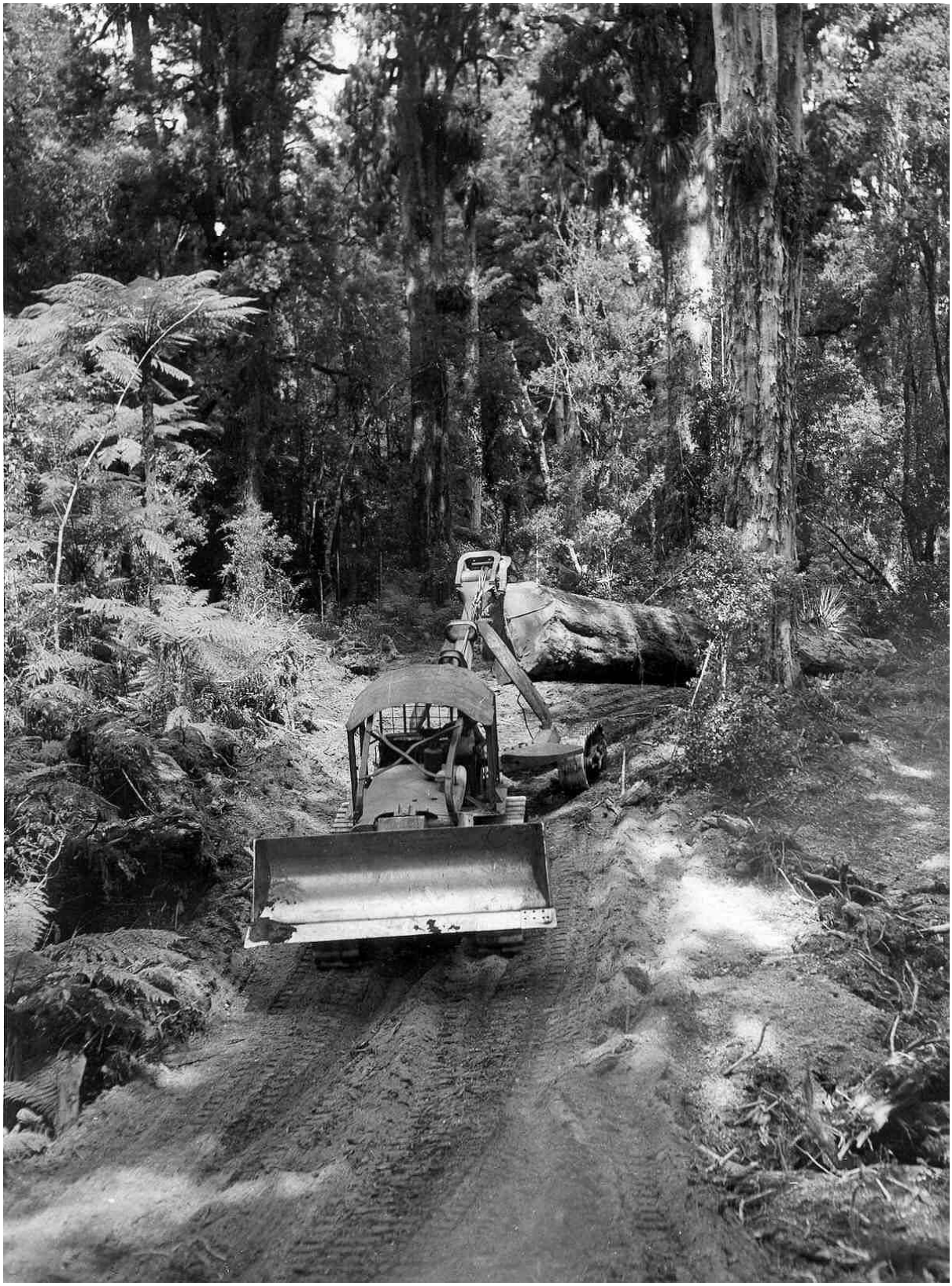

Figure 62. Hauling of *Dacrydium cupressinum* in podocarp-broadleaved forest at Pureora using a Caterpillar RD8 Diesel tractor and a Hyster 20 ton crawler logging arch (The Fletcher Archives, 1956).

4.2.2. Research setup

This study of the effect of canopy disturbances of different scales on long-term tree species recruitment focuses mainly on the podocarp species *D. dacrydioides*, *D. cupressinum*, *P. totara*, *Phyllocladus trichomanoides*, *P. ferruginea* and *P. taxifolia* as well as the angiosperms *B. tawa* and *Elaeocarpus dentatus*, but incorporates all tree and tree fern species that were found in gaps. A more detailed description of those species is given by Dawson (1988), Dawson & Lucas (2011) and Wardle (2011) as well as in Table 7.

Harvesting inventory

While the pre-harvesting frequency and abundance of emergent podocarps is well documented for the FRI blocks, no information is available for the Māori blocks. To get an approximation of the pre-harvesting distribution of emergent podocarps there, an inventory was carried out based on tree stump recordings in 58 circular plots of 40 m diameter. These 'stump' inventories are generally used for stump harvesting operations (Berch et al., 2012) or in the context of forest health studies (Huse, Solheim, & Venn, 1992). Even 56 years after harvesting, stumps of harvested trees are still very visible due to the relatively low decomposition rates of the tree species in focus (Figure 63).

Figure 63. Stump of an emergent podocarp (dbh≈ 140 cm) harvested in the Wharepuhunga -Pouakani-Maraeroa block in 1956/58; the ranging pole next to the stump is 2 m long (photo taken in 2014, 56 years after harvesting)

Beets et al. (2008) calculated the average decomposition rates of stems, with wood losing 50 % of its mass ($t_{1/2}$) for *D. dacrydioides* (14 years), *D. cupressinum* (18 years), *P. ferruginea* (16 years), *P. taxifolia* (39 years) and *B. tawa* (26 years).

But depending on the species of decay fungi colonizing the wood, mean $t_{1/2}$ can take between 20 and 40 years. The size of trees also plays an important factor in decay rates, with larger diameter trees decaying more slowly than smaller diameter trees. To get an approximation of dimensions of harvested trees in case they were cut below breast height, the strong linear relationship (r^2 = 0.96) between diameter in stump height (*dsh* = 0.3 m above ground) and diameter in breast height (dbh = 1.4 m above ground) with *dbh = 0.92 + 0.90*dsh* that was found by Mansell (2005) for *D. cupressinum* at Pureora, was used to estimate dbh. Due to the expected decay of bark and sapwood, stump diameter estimates were grouped into 20 cm-classes.

Disturbance and gap size

The gap phase represents the most dynamic phase in a forest (Watt, 1947). Light-demanding podocarp species such as *D. dacrydioides* and *P. totara* as well as relatively shade-resistant species such as *D. cupressinum* and *P. ferruginea* are believed to require increased light levels for subsequent growth (Ebbett & Ogden, 1998; Lusk et al., 2009). The size of a canopy gap determines the scale of change in the light environment (Poulson & Platt, 1989). Traditionally, gaps are regarded as small-scale disturbances that are created by single tree or small group death of main canopy trees and expose the understorey of a forest to the sky (Runkle, 1982). The maximum diameter of a gap is often restricted to 10 trees or a canopy height – gap diameter ratio of 1.0 (Runkle, 1992). Canopy openings larger than 1000 m² are generally not considered as gaps any more as they were found to generate microclimates substantially different from gaps (Schliemann & Bockheim, 2011). However, some research on gap dynamics was found to include canopy openings up to 10 000 m² (Kathke & Bruelheide, 2010). In case of the present study, which is comparing the effect of different scales of canopy disturbance (from single tree to large-scale) on tree species regeneration and composition in gaps, the maximum size recorded was set to a circular plot of 40 m diameter, which corresponds to the height of the large emergent podocarps.

There is no consistent methodology of estimating the size of a gap. In general, three approaches are used: two and three dimensional vertical projections based on ground measurements (Runkle, 1981), vertical projection based on aerial photography (Kathke & Bruelheide, 2010) and ground based hemispherical photography (Rich, 1990; Yamamoto, 2000). The most common methods involve various forms of ground measurements (Schliemann & Bockheim, 2011). While some authors use only two measurements, the largest length of a gap plus the width perpendicular to that length (Runkle, 1981), others measure the distance from the centre of a gap to its edge in form of polar coordinates with 8 (Brokaw, 1982) or 16 measurements (Green, 1996) respectively. On the other hand, De Lima (2005) proposes a method, where the gap is divided into irregular triangles.

The method used in the present study is a combination of several measures, as gaps were created several decades ago (Figure 64). Canopy gaps were randomly selected and all trees were recorded with species, diameter, social class and polar coordinates in concentric sampling plots with a maximum of 40 m diameter. Then crown projection measurements of all mature social class 1 and 2 trees were taken using the method described by Röhle (1986) and heights of the surrounding main canopy were measured. This methods was used instead of the expanded gap method proposed by Runkle (1982) as large crowns of gap-demarcating trees would have otherwise obscured the actual gap size (M. C. Smale & P. N. Smale, 2003). Based on those parameters, a tree location map was plotted showing the exact location of every tree within the plot. At least 2 trees of each social class of the species in focus were cored to get estimates of gap age and to investigate gap dynamics. In addition, trees were identified that were already part of the main canopy before the disturbance and gap size measurements were adjusted by adding additional crown projection measurements.

The canopy periphery was then demarcated using these parameters. To allow for maximum irregularity of gap forms while maintaining a simple gap measurement method, the two-dimensional gap size was calculated with the help of 32 polar coordinates from the centre to the periphery of the gap. This way, the maximum calculated gap size will be 1249 m^2 even though a 40 m circle has a size of 1256.6 m^2. To limit sampling effort within a plot while maximizing the number of observations in different plots, this study focuses on the effect of

past disturbances on the inner 24 m diameter circular plot. In a preliminary study, this was found to be the maximum height of trees in closed gaps.

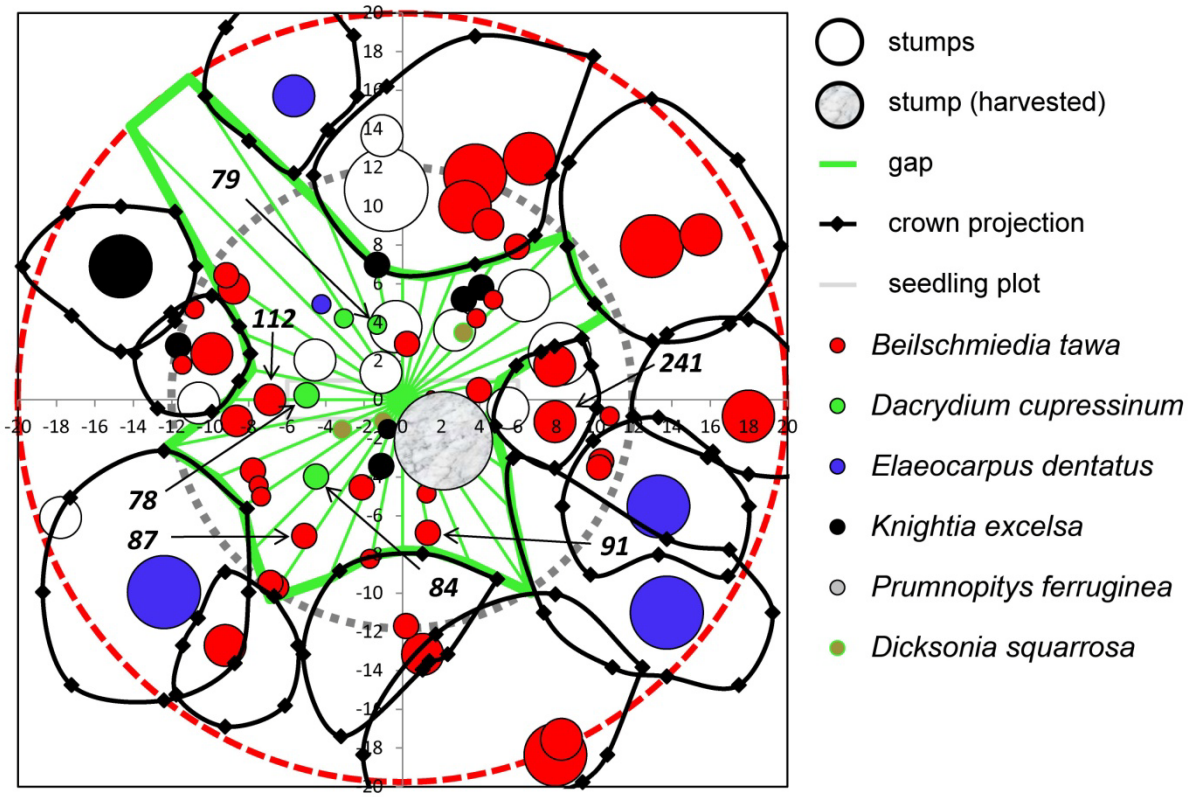

Figure 64. Tree location map (Ø 40 m) with crown projection of dominant social class 1 and 2 trees, 32-point gap measurement and age of cored trees; different colours of circles show different tree species and their size relates to their diameters

Composition and structure

This part of the study followed the general plot design elaborated in Chapter 3. But while the above design focused on the dynamics of old-growth forest, in this chapter the effect of disturbances of different scales on forest composition and structure is investigated. Therefore, 106 sampling points were established in the two Māori blocks, the FRI blocks and the adjacent old-growth forest (Table 35). Obvious signs of soil disturbance such as skidder tracks or hauling sites were excluded from this study.

Table 35. Number of sampled plots at the different sites

Study site	No. of plots
Old-growth forest	32
Selective harvesting (FRI blocks)	16
High-grading (Māori blocks)	56
total:	**106**

Species responses to the canopy gap-size gradient were modelled in two steps using incidence first and secondly, abundance data. Presence – absence data was investigated separately, as species abundances are more likely to be influenced by a broad range of unmeasured site factors (i.e., dispersal, biotic interactions) (Boulangeat, Gravel, & Thuiller, 2012) which might introduce pronounced noise in the analysis (J. B. Wilson, 2012). Species abundances were then analysed only for sampling plots where the specific species was present, i.e., plots with zero abundances were excluded. Species response curves were fitted for the binary incidence data set using generalized linear models (GLM) with a binominal error distribution and logit link function. Ecological theory (Austin, 2013; Whittaker, 1978) and research (Oksanen & Minchin, 2002; Olthoff, Martínez-Ruiz, & Alday, 2016) suggests that most species distribution curves along environmental gradients are unimodal ('humpbacked' response). Therefore a second order polynomial was fitted for gap-size. For the abundance data three GLMs with 1 to 3 polynomial degrees for gap size were fitted using a Poisson distribution (log link). The best model was determined based on the lowest Akaike information criterion (AIC) (Akaike, 1974). All species response curves were drawn using function 'specresponse' from the package goeveg (Goral & Schellenberg, 2017).

Age structure

One objective of this study was to identify the effect of harvesting on trees species regeneration. Different tree species have different dispersal methods, and light and shelter requirements for successful regeneration and subsequent growth. It was expected that shade-tolerant trees do not need substantial canopy openings for subsequent growth. But light-demanding tree species that need substantial canopy openings for regeneration were expected to have become established in large gaps after gap formation. It was also of interest, if trees in harvesting gaps belong to a single cohort that established at the same time or if they have established continuously over time. Therefore, 372 trees of all podocarp species as well as the angiosperms *B. tawa* and *E. dentatus* from different size harvesting gaps were cored in 0.3 m height (Figure 65, Table 36). The approximate age and years of establishment of those trees were estimated following the method described in Chapter 2. Mixed-effect models that include the sampling plot as a random effect and estimated tree ages as fixed effects were used to model the relationship between tree age and gap size.

Figure 65. Tree coring of *Beilschmiedia tawa* in 0.3 m height

Growth analysis

From all sampled gaps in the old-growth forest, the selectively logged forest and the high-graded forest, a total number of 499 tree cores were taken at 0.3 m coring height randomly from all podocarp species as well as *B. tawa* and *E. dentatus* across all social classes (Table 36). The objective was to estimate past periodic mean annual diameter increments (*mai*) as well as to identify growth patterns. The relationship between *mai* and gap size was modelled using mixed effect models that incorporate the sampling plots as random effects and *mai* as the fixed effect.

Table 36. Number of tree cores taken from the different species and at the different sites

Species	Old-growth	High-grading	Selective	total
Dacrycarpus dacrydioides	3	5	-	8
Dacrydium cupressinum	17	112	10	139
Phyllocladus trichomanoides	-	3	3	6
Podocarpus totara	-	11	-	11
Prumnopitys ferruginea	39	97	21	157
Prumnopitys taxifolia	-	7	-	7
Beilschmiedia tawa	35	38	20	93
Elaeocarpus dentatus	33	36	9	78
total:	**127**	**309**	**63**	**499**

A changepoint analysis of the cored trees in harvesting gaps of the Māori blocks was used to detect individual growth release and suppression patterns as elaborated in Chapter 2. Of particular interest was here if large-scale disturbances led to changepoints of growth shared by multiple trees across the high-graded blocks.

4.3. Results

4.3.1. Harvesting intensity

The calculated numbers of harvested trees per hectare based on tree stump counts and measurements in the Māori blocks indicate that these blocks had a distribution of large podocarps that was similar to the adjacent old-growth and FRI blocks (Table 37). The calculated standard error shows that these podocarps were not evenly distributed within the forest, with calculated abundances ranging for from 8 to 56 trees ha^{-1}. In some sampling plots, no podocarps of diameters >40 cm were present at the time of harvesting and the forest canopy remained undisturbed by harvesting. At other sites, up to 7 stumps of harvested large podocarps were found in plots of 40 m diameter.

Table 37. Abundance of large podocarps in blocks A-C and modelled number of podocarps in the high-graded Māori blocks

Block	size (ha)	trees ha^{-1}	SE
Old-growth (block A)	15	25	
Selective harvesting (block B)	15	26	
Selective harvesting (block C)	15	21.2	
High-graded (Māori blocks)	100	25.8	3.8

Accounting for wood decay over the past 56 years and the differences between diameter in breast height and diameter in stump height, tree diameters were assigned to 20 cm classes. Diameter distributions of large podocarps in the blocks A-C were similar to the distributions calculated for the Māori blocks (Figure 66). Only in the smallest class that incorporates all stumps up to 60 cm diameter were the calculated values in the Māori blocks more than twice as large as in the other blocks. In all blocks, podocarps of diameters >40 cm showed bell-shaped distributions, with similar means of 97.2 cm in the A-block, 102.9 cm in the B-block, 97 cm in the C-block and 104.95 cm in the Māori blocks. But the variation in diameter classes was high between plots, and standard errors ranged from 0.4 to 1.7. With podocarps of diameters >160 cm being rare, the standard errors were particularly large in those diameter classes.

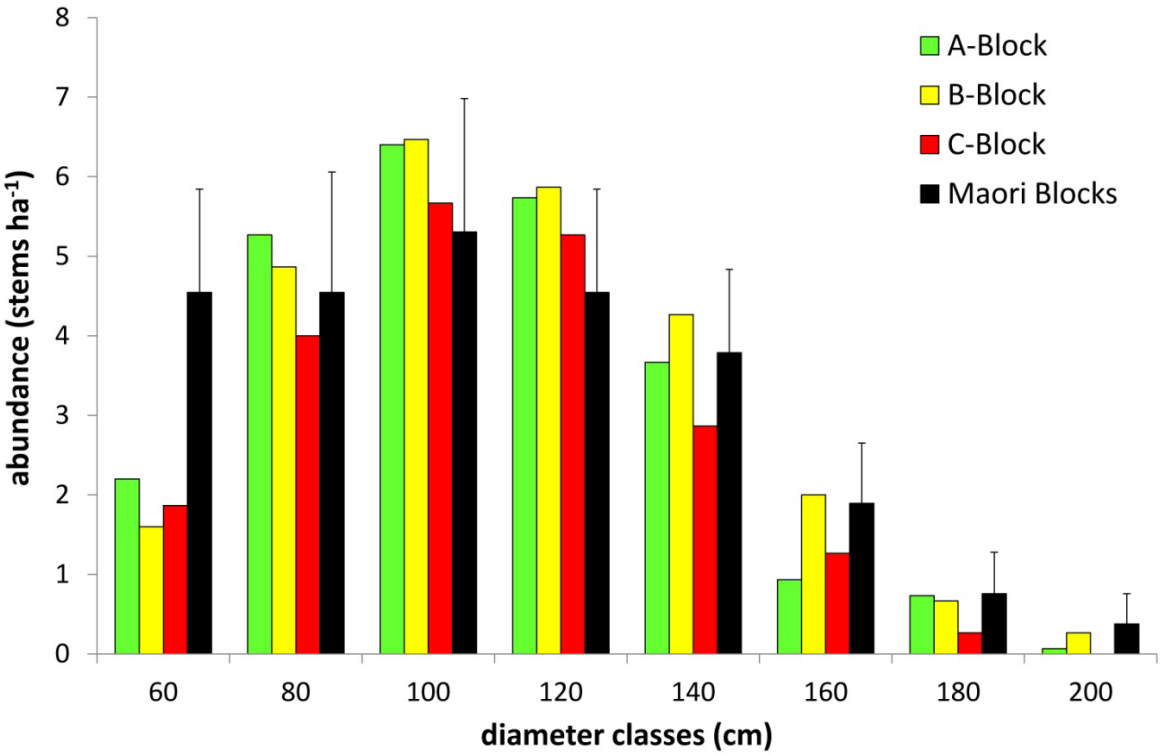

Figure 66. Pre-harvesting abundance of podocarps of different diameter classes in the different forest blocks; the abundances for the Māori blocks including SE are calculated on the basis of stumps of harvested trees; class names correspond to the upper class limit

4.3.2. Canopy gap sizes

The frequencies of different size gaps varied between old-growth forest, selectively logged forest and high-graded forest (Figure 67). Natural gaps in old-growth forest ranged from 57 to 1049 m² with 70% of the gaps being smaller than 402 m². The canopy gap sizes in selectively logged forest ranged from 117 to 826 m² with 70 % being between 372 and 724 m². In the high-graded forest, gaps ranged from 36 to over 1249 m² with 70 % being between 720 and over 1249 m². This was the chosen upper limit of gap measurements even though 16 % of the gaps were actually larger than 1249 m². In those cases, high-grading resembled the effect of clear-felling with few residual trees left.

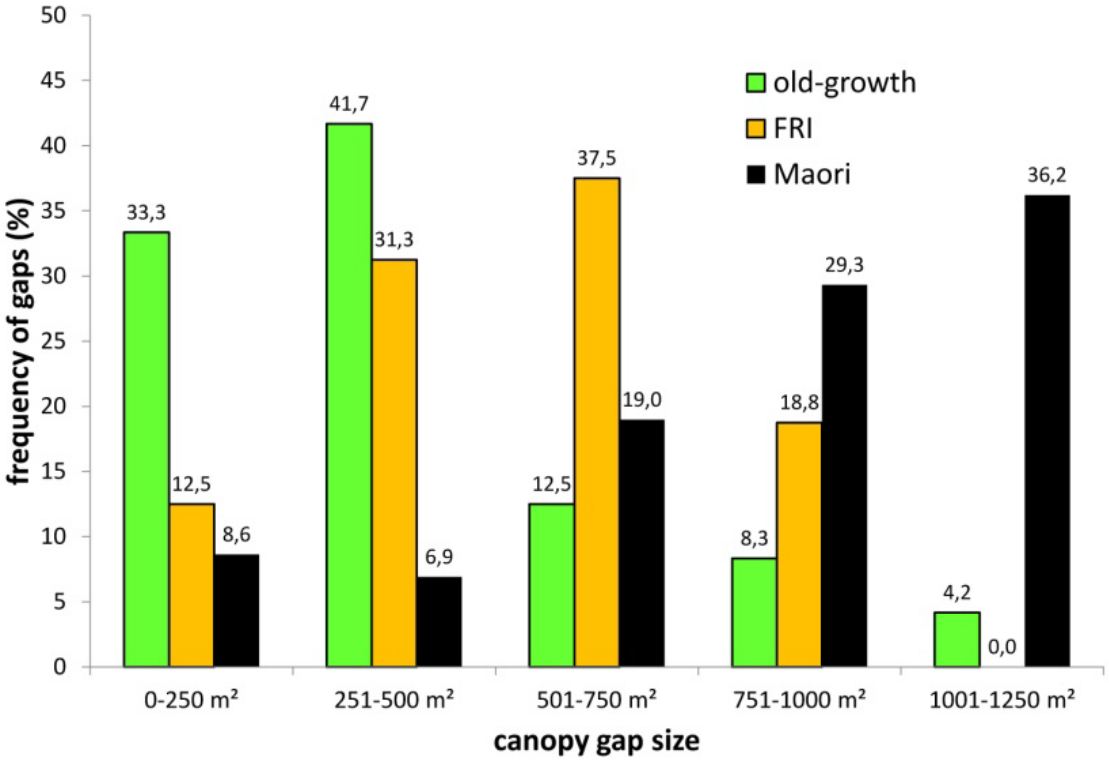

Figure 67. Frequency of different size canopy gaps in old-growth forest, selectively logged forest (FRI) and high-graded forest (Māori)

4.3.3. Species frequencies

Using 5416 measured trees in 106 sampled gaps, the relationship between the presence of tree species and gap size was analysed based on logistic regression using Generalised Linear Models (Table 38). All podocarp species except *D. dacrydioides* and *P. trichomanoides* showed significant ($p<0.05$) positive correlations. This relationship was strongest for *D. cupressinum*, followed by *P. ferruginea* and *P. taxifolia*. Among the larger angiosperm tree species, only *B. tawa* and *E. dentatus* showed significant correlations between species presence and gap size. This relationship was negative for *B. tawa* but positive for *E. dentatus*, where the periodic annual mean increment (52 years) increased with increasing gap size. Six out of 19 smaller tree species showed a significant positive correlation between species presence and gap size, with *P. crassifolius*, *C. serratus*, *P. arboreus, W. racemosa* and *C. australis* showing the strongest relationship. No negative correlation could be found for any of the smaller tree species. The tree fern species *D. fibrosa* showed significant positive relationship between species presence and gap size, while this and *D. squarrosa* showed a

significant negative correlation. The relationships for *C. dealbata* and *C. smithii* were not significant.

Table 38. Relationships between the occurrence of 31 tree species and 4 tree fern species and gap size in 106 gaps; results are based on generalized linear models with binomial error distribution; modelling is based on measurements of 5416 trees; blue numbers show significant positive relationships; red numbers show significant negative relationships; n = number of gaps where a species was present

Gymnosperms	χ^2	p	SE (poly 1)	SE (poly 2)	pseudo r^2	*n*
Dacrycarpus dacrydioides	3.84	0.18	8.47	7.10	0.07	7
Dacrydium cupressinum	**29,60**	**<0.01**	**3.11**	**2.88**	**0.20**	**51**
Phyllocladus trichomanoides	1.07	0.40	4.93	4.81	0.02	7
Podocarpus totara	5.67	0.13	9.39	6.55	0.10	8
Prumnopitys ferruginea	**30,13**	**<0.01**	**2.47**	**2.75**	**0.23**	**73**
Prumnopitys taxifolia	8.90	0.06	6.39	4.78	0.13	10
Angiosperms (large trees)						
Beilschmiedia tawa	**10.72**	**<0.01**	**2.57**	**3.02**	**0.13**	**92**
Elaeocarpus dentatus	**12.80**	**<0.01**	**2.13**	**2.30**	**0.10**	**73**
Elaeocarpus hookerianus	3.93	0.09				4
Knightia excelsa	0.45	0.60	3.72	3.66	0.01	9
Nestegis cunninghamii	0.02	0.88				2
Nestegis lanceolata	4.04	0.08	2.97	2.94	0.04	22
Angiosperms (small trees)						
Aristotelia serrata	2.33	0.14				11
Carpodetus serratus	**35.35**	**<0.01**	**3.11**	**2.95**	**0.24**	**47**
Cordyline australis	**37.98**	**0.05**	**15.65**	**8.75**	**0.37**	**21**
Griselinia littoralis	19.47	0.31	105.47	41.63	0.38	7
Griselinia lucida	0.06	0.81				2
Hedycarya arborea	1.76	0.19				7
Kunzea ericoides s.l.	15.52	0.11	20.10	10.86	0.22	11
Melicytus ramiflorus	0.05	0.82	2.36	2.37	0.01	24
Melicytus lanceolatus	-	-	-	-	-	1
Myrsine australis	-	-	-	-	-	1
Pennantia corymbosa	**8.48**	**0.05**	**6.40**	**4.74**	**0.11**	**12**
Pittosporum tenuifolium	9.43	0.02	52.35	24.16	0.23	5
Pseudopanax arboreus	**29.94**	**<0.01**	**2.71**	**2.66**	**0.20**	**51**
Pseudopanax crassifolius	**36.12**	**<0.01**	**3.14**	**2.99**	**0.25**	**55**
Raukaua edgerleyi	2.48	0.13				9
Pseudowintera colorata	0.40	0.54				4
Quintinia serrata	-	-	-	-	-	1
Schefflera digitata	0.58	0.46				6
Weinmannia racemosa	**7.13**	**0.01**	**2.13**	**2.13**	**0.05**	**58**
Tree ferns						
Cyathea dealbata	5.31	0.08	5.95	4.75	0.09	9
Cyathea smithii	1.05	0.34	2.04	2.04	0.01	49
Dicksonia fibrosa	**17.90**	**<0.01**	**2.65**	**2.52**	**0.13**	**34**
Dicksonia squarrosa	**3.92**	**0.04**	**2.28**	**2.42**	**0.04**	**85**

The calculated pseudo R squared values for the different species appeared to be low at first glance, but it has to be remembered that these are McFadden's pseudo R squared measures which are always much lower than R squared values in ordinary least squares (OLS) models; values between 0.2 and 0.4 are considered to be of excellent fit (McFadden, 1973).

Fitting the probabilities of occurrence of the different tree species in different size gaps in the form of species response curves shows that they do not only have different frequencies of occurrence but also different unimodal distributions (Figure 68). Shade-tolerant *B. tawa* is the most frequently occurring tree species with a maximum probability of 95.6 % (± 2.4) at a gap size of 616 m². It appears in more than 80 % of the gaps between 100 and 1100 m². *Prumnopitys ferruginea* is the second most frequent tree species with a maximum probability of 89.4 % (± 3.8) at a gap size of 800 m², followed by *E. dentatus* (83.6 % ± 4.8 at 741 m²) and *D. cupressinum* (72.2 % ± 6.1 at 1042 m²). *Nestegis lanceolata* mainly occurs in medium-sized gaps with a maximum of 29.5 % (± 6.8) at 596 m², while *P. taxifolia* is associated with the largest gaps and shows a maximum probability of 29.1 % (± 12.4) in the largest gaps of 1249 m².

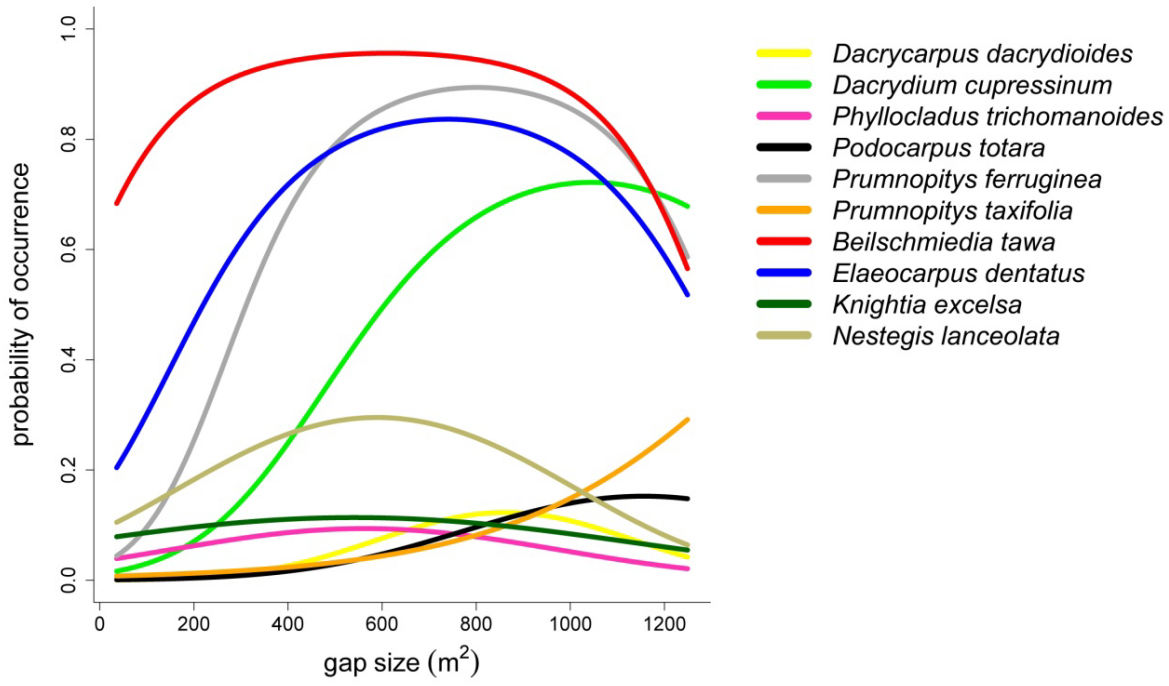

Figure 68. Probability of occurrence of main canopy tree species in gaps of different sizes

All other main canopy tree species were scarce with *P. totara* showing a maximum probability of 15.3 % (± 6.7) at 1152 m², *D. dacrydioides* with 12.3 % (± 5.3) at 858 m², *K. excelsa* with 11.4 % (± 4.5) at 551 m² and *P. trichomanoides* with 9.4 % at 568 m² (± 4.4).

With the exception of *M. ramiflorus*, all subcanopy species showed an increase in occurrence with increasing gap size. The probability of occurrence was strongest for *P. arboreus* (89.9 % ± 6.5 at 1249 m²), *C. serratus* (85.4 % ± 8.2 at 1249 m²) and *P. crassifolius* (80 % ± 7.5 at 1152 m²) (Figure 69). *Weinmannia racemosa* had a maximum probability of occurrence of 67.4 % (± 10.0) at 1212 m² but was also present in over 20 % of the smallest gaps. *Melicytus ramiflorus* did not show a significant response to gap size, occurring in all gap sizes similar frequently and with a slight maximum of 24.6 % (± 10.7) at 1249 m². All other small tree species do not appear in small gaps below 500 m². The strongest increase of those species in frequency with increasing gap size was observed for extremely light-demanding *C. australis*, with a maximum probability of 68.0 % (± 13.0) at 1249 m² gap size. *Pennantia corymbosa* (26.3 % ± 11.8 at 1249 m²) and *Kunzea ericoides s.l.* (28.9 % ± 9.5 at 1192 m²) show similar relationships. *Griselinia littoralis* appeared only in the largest gaps and reached a maximum of 32.7 % (± 13.5) at 1249 m² gap size. The rarest of the small tree species was *P. tenuifolium* with a maximum probability of 16.9 % (± 8.2) at 1192 m².

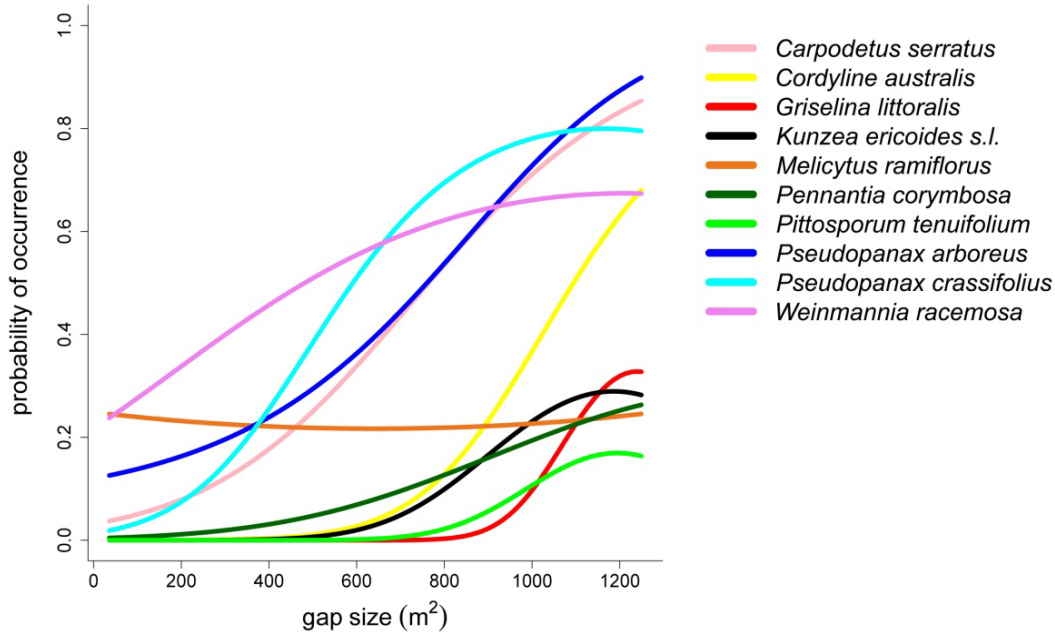

Figure 69. Probability of occurrence of small tree species in gaps of different sizes

The species response curves for the 4 tree fern species that occur at the study site show that *D. squarrosa* and *C. smithii* have similar shapes of unimodal distributions, even though they have different probabilities (Figure 70). *Dicksonia squarrosa* was the most frequently present tree fern species with a maximum probability of 87.5 % (± 4.3) at a gap size of 676 m², at which stage it begins to decline in occurrence. *Cyathea smithii* appeared less frequently with a maximum of 51.3 % (± 7.0) at 616 m² gap size. But this relationship was not found to be significant. A strong positive correlation between probability of occurrence and gap size was found for *D. fibrosa* with a maximum of 70.1 % (± 11.2) at 1249 m². *Cyathea dealbata* was the least frequently occurring tree fern species that occurred in only 9 plots. According to those few observations the relationship between species occurrence and gap size was slightly negative with a maximum probability of 19.5 % (± 14.3) at the smallest gap size of 36 m².

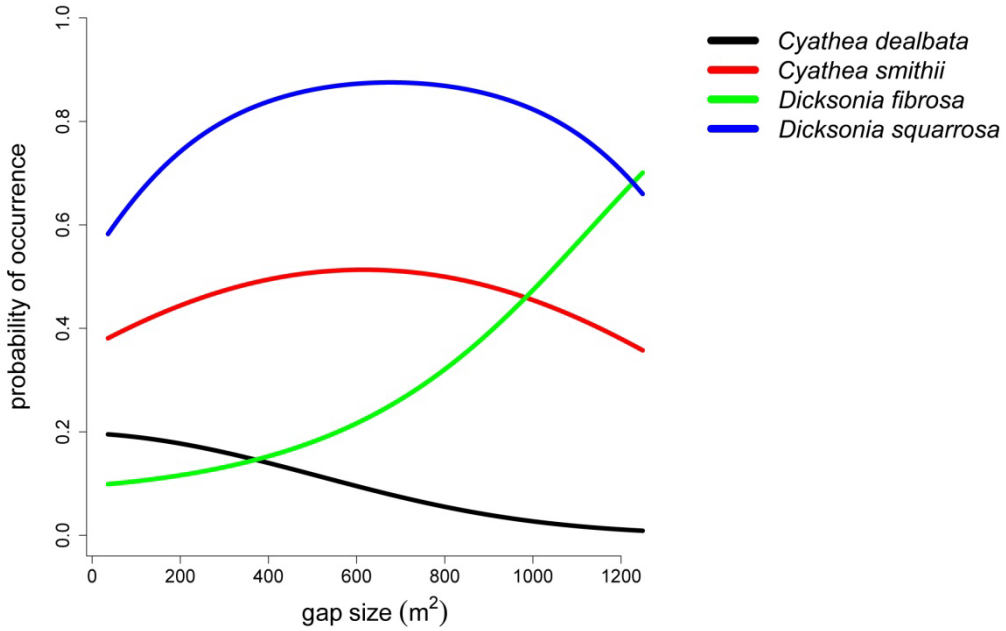

Figure 70. Probability of occurrence of 4 tree fern species in gaps of different sizes

The above analysis used species presence as the response variable to investigate the effect of gap size. It did however not differentiate between the sizes of trees that occur. This means that a small tree of 2 cm diameter has the same effect in the model as a large tree of 40 cm. To account for the different dimensions of trees that are found in gaps, they were divided into 5 different diameter classes and frequencies of presence were calculated for 5

gap size classes (Table 39). Eleven tree species were found in the smallest gap size class (0-250 m²). They represent the most shade-tolerant species in the forest, with the angiosperm *B. tawa* occurring frequently in diameter classes 1 and 2 but being two times less frequent in diameter class 3. Other shade-tolerant angiosperms frequently occurring in diameter classes 1-3 are *E. dentatus* and *W. racemosa*. *Prumnopitys ferruginea* is the most shade-tolerant podocarp species and occurred in 13 % of the gaps but only in diameter class 2. The other species were found only infrequently in the different diameter classes.

Table 39. Frequency (%) of gaps in different gap size classes (0 – 250 m²; 251 – 500 m²; 501 – 750 m²; 751 – 1000 m²; 1001 – 1250 m²) where 31 tree species in different diameter classes occur (1 = 0 – 9.9 cm; 2 = 10.0 – 19.9 cm; 3 = 20.0 – 29.9 cm; 4 = 30.0 – 39.9 cm; 5 = 40.0 – 49.9 cm); total occurrence of each species in different gap size classes are written in *italic*

	0 – 250 m²				251 – 500 m²					501 – 750 m²						751 – 1000 m²						1001 – 1250 m²					
Gymnosperms	**1**	**2**	**3**	***total***	**1**	**2**	**3**	**4**	***total***	**1**	**2**	**3**	**4**	**5**	***total***	**1**	**2**	**3**	**4**	**5**	***total***	**1**	**2**	**3**	**4**	**5**	***total***
Dacrycarpus dacrydioides					5				***5***	8					***8***	5	5	9			***9***	8	4	4			***8***
Dacrydium cupressinum					25	25	25	15	***30***	40	52	16	4		***56***	50	50	32	9		***64***	46	63	38	21		***71***
Phyllocladus trichomanoides		7		***7***		5	5		***10***	4	8		4		***12***							4	4				***4***
Podocarpus totara							5		***5***		4	4			***4***	5	9				***9***	8	13				***17***
Prumnopitys ferruginea		13		***13***	40	65	35		***70***	48	60	40	4		***84***	41	68	55	9		***82***	38	63	50	4		***75***
Prumnopitys taxifolia					5				***5***	8					***8***	5					***5***	8	8	13	4		***25***
Angiosperms (large trees)																											
Beilschmiedia tawa	60	67	20	***80***	65	95	40	10	***95***	68	84	56	16		***96***	36	73	41	5		***82***	42	63	33		4	***75***
Elaeocarpus dentatus	7	20	20	***40***	5	45	35	15	***55***	24	72	52	20	8	***88***	18	59	32	18	5	***73***	17	46	17	17		***54***
Elaeocarpus hookerianus						5			***5***								9	5			***9***		4	4			***8***
Knightia excelsa		7		***7***		15	5		***15***								9	5	5		***18***				4		***4***
Nestegis cunninghamii					5				***5***															4			***4***
Nestegis lanceolata		7		***7***	20	20			***35***	8	20	8			***24***		23				***23***	4	8				***13***
Angiosperms (small trees)																											
Aristotelia serrata					15				***15***	4	4				***8***	9					***9***	13	4				***17***
Carpodetus serratus					15	10			***25***	24	40				***44***	23	45	18			***50***	54	79	29			***83***
Cordyline australis											8				***8***	5	9	5	5		***9***	8	38	46	17		***50***
Griselinia littoralis																	5				***5***	13	17				***25***
Griselinia lucida							5		***5***	4	4				***4***												
Hedycarya arborea	7	7		***7***	5	10			***10***	12		4			***12***							4	4				***4***
Kunzea ericoides s.l.											4				***4***	5	14				***18***	17	8				***21***
Melicytus ramiflorus		7	7	***13***		25	15		***30***		12	8			***20***		23	9			***23***	8	17	8			***25***
Melicytus lanceolatus																						4					***4***
Myrsine australis						5			***5***																		
Pennantia corymbosa							5		***5***	4	4				***4***		9	9			***14***	8	25				***25***
Pittosporum tenuifolium																	5				***5***	4	4	13			***17***
Pseudopanax arboreus		13		***13***	5	15			***15***	24	40	20			***44***	45	64	23			***73***	50	71	21			***83***
Pseudopanax crassifolius			7	***7***	5	15		5	***25***	20	52	8			***56***	14	73			5	***73***	54	75	21			***79***
Raukaua edgerleyi										8	12	4			***16***	9	5				***14***	8	4				***8***
Pseudowintera colorata										12					***12***							4					***4***
Quintinia serrata						5			***5***		4				***4***												
Schefflera digitata					5	5			***10***		4				***4***							4	4				***8***
Weinmannia racemosa	7	20	13	***33***	15	35	5		***45***	16	52	4			***60***	14	59	9			***64***	29	54	8			***63***

In the second gap size class (251 – 500 m²), the most frequent species was again extremely shade-tolerant *B. tawa*. In this gap size class, shade-tolerant *P. ferruginea* increased in presence from 13 to 70 % of gaps now covering diameter size classes 1-3. The intermediate shade-resistant podocarp species *D. cupressinum* was present in all diameter classes up to class 4. The other podocarp species now also began to appear infrequently. The main angiosperm tree species in this gap size class were again *E. dentatus*, *W. racemosa* and *M. ramiflorus*. While the main presence of *B. tawa* and *P. ferruginea* was concentrated in diameter classes 1 and 2, *E. dentatus* was mainly found in diameter classes 2 and 3. Other intermediate light-demanding tree species such as *P. arboreus*, *Pseudopanax crassifolius* and *Carpodetus serratus* became established more frequently. Even species that are relatively light-demanding such as *Nestegis lanceolata* were already present in diameter classes 1-2 in larger gaps of this gap size class.

In the third gap size class (501 – 750 m²) almost all species increased in their frequency of occurrence. *Beilschmiedia tawa* was once more the most frequent tree species occurring in 96 % of the gaps. This means that *B. tawa* was present in every gap but one, with a peak in diameter class 2. Species with the largest increase in presence of all diameter classes were *E. dentatus* which extended even into diameter class 5, the podocarps *D. cupressinum* and *P. ferruginea* and the smaller tree species *C. serratus*, *P. arboreus*, *P. crassifolius* and *W. racemosa*.

With gap sizes increasing further to 751 – 1000 m², the frequencies of plots where the shade-tolerant angiosperm species *B. tawa*, *E. dentatus* as well as the podocarp species *P. ferruginea* occur began to decrease, while the presence of almost all other tree species increased further. The main diameter classes were again classes 1-3 for all species. Trees of diameter classes 4-5 were found only infrequently, with *E. dentatus* still being the most frequent species in these diameter classes.

This trend of increasing presence in gaps continued in the largest gap size class (1001 to 1250 m²) for all species except *P. ferruginea*, *B. tawa* and *E. dentatus*. Their relationship continued to be negative in this gap size class. *Carpodetus serratus* and *P. arboreus* were

now the most frequently occurring species and were found in 83 % of the gaps. In this class, the podocarp species *D. cupressinum* and *P. ferruginea* showed a distribution similar to *B. tawa*, with a peak in diameter class 2. Other species found frequently in this largest gap size class were *P. crassifolius*, *W. racemosa* and *C. australis*.

Dicksonia squarrosa was the most frequently occurring tree fern species in all gap size classes, being present in 67-88 % of the gaps (Table 40). The least frequently occurring tree fern species was *C. dealbata* and showed a negative correlation with gap size. *Cyathea smithii* did not show a correlation between presence in gaps and gap size while the presence of *D. fibrosa* increased with gap size.

Table 40. Frequency (%) of gaps in different gap size classes (0 – 250 m²; 251 – 500 m²; 501 – 750 m²; 751 – 1000 m²; 1001 – 1250 m²), where the different tree fern species occur

Fern species	0 – 250 m²	251 – 500 m²	501 – 750 m²	751 – 1000 m²	1001 – 1250 m²
Cyathea dealbata	20	10	12	5	
Cyathea smithii	53	35	48	50	38
Dicksonia fibrosa	20		24	41	63
Dicksonia squarrosa	67	85	88	82	71

The next step was an analysis of the relationship between the presence of trees of different social classes and gap size (Table 41). Significant positive relationships were found for the podocarps *D. cupressinum* and *P. ferruginea* in all social classes and for the angiosperm *E. dentatus* in classes 3 and 4. Significant positive relationships were also found for the five most common subcanopy angiosperm tree species *C. australis*, *P. arboreus*, *C. serratus*, *P. crassifolius* and *W. racemosa*. Dominated understorey trees shared this relationship only in the case of *P. crassifolius*. The shade-tolerant species *B. tawa* showed a significant negative relationship between species occurrence and gap size in all social classes. The only other species with a significant negative relationship was the shade-tolerant tree fern species *Cyathea dealbata*, which only occurred in social class 5. Significant positive relationships were found for the tree fern species *D. fibrosa* in social class 5 and for *D. squarrosa* in social class 4. *Melicytus lanceolatus* did not occur in numbers that allowed this analysis. Besides the different tree and tree fern species displayed in Table 41, a number of small leaved shrub species of the genus Coprosma were present in several gaps. They included *Coprosma crassifolia*, *Coprosma dumosa*, *Coprosma propinqua*, *Coprosma rhamnoides* and *Coprosma*

rotundifolia as well as *Coprosma robusta* and *Coprosma grandifolia*. Other species found in gaps were *Leptospermum scoparium* and *Olearia rani*. But as this study focuses on tree species, no further analyses of presence and abundance of shrub species were carried out.

Table 41. Relationship between the occurrence of 35 tree species and gap size in 106 gaps based on generalized linear models with binomial error distribution; modelling is based on measurements of 5416 trees of three social classes; blue numbers show significant positive relationships; red numbers show significant negative relationships; pR^2 is McFadden r-square

	social class 3			social class 4			social class 5		
Gymnosperms	χ^2	p	pR^2	χ^2	p	pR^2	χ^2	p	pR^2
Dacrycarpus dacrydioides	5.28	0.23	0.19	1.45	0.36	0.04	2.62	0.37	0.10
Dacrydium cupressinum	**22.63**	**<0.01**	**0.16**	**20.11**	**<0.01**	**0.14**	**11.29**	**0.02**	**0.10**
Phyllocladus	0.32	0.57		0.15	0.74	<0.01	-	-	
Podocarpus totara	6.39	0.19	0.16	2.59	0.24	0.06	3.23	0.34	0.16
Prumnopitys ferruginea	**23.60**	**<0.01**	**0.16**	**11.06**	**0.01**	**0.08**	**15.82**	**<0.01**	**0.12**
Prumnopitys taxifolia	14.58	0.47	0.36	7.72	0.26	0.23	2.34	0.25	0.07
Angiosperms (large trees)									
Beilschmiedia tawa	**14.95**	**<0.01**	**0.10**	**6.89**	**0.03**	**0.06**	**5.68**	**0.02**	**0.04**
Elaeocarpus dentatus	**13.16**	**<0.01**	**0.09**	**11.02**	**<0.01**	**0.08**	3.21	0.13	0.05
Elaeocarpus hookerianus	0.80	0.40		4.03	0.16		-	-	
Knightia excelsa	0.03	0.87		2.92	0.24	0.09	-	-	
Nestegis cunninghamii	1.15	0.38		0.65	0.46		-	-	
Nestegis lanceolata	0.4	0.58	0.01	6.08	0.05	0.06	0.45	0.53	<0.01
Angiosperms (small trees)									
Aristotelia serrata	2.86	0.15		1.93	0.18		0.61	0.45	
Carpodetus serratus	**38.33**	**<0.01**	**0.31**	**34.59**	**<0.01**	**0.24**	2.78	0.17	0.06
Cordyline australis	**46.98**	**0.04**	**0.52**	13.02	0.09	0.18	-	-	
Griselinia littoralis	-	-		13.18	0.18	0.33	-	-	
Griselinia lucida	<0.01	0.93		0.13	0.72		-	-	
Hedycarya arborea	0.03	0.86		2.99	0.11		0.05	0.83	
Kunzea ericoides s.l.	12.28	0.09	0.24	9.03	0.22	0.22	-	-	
Melicytus ramiflorus	1.21	0.40	0.04	0.48	0.56	<0.01	1.24	0.32	0.03
Melicytus lanceolatus	-	-		-	-		-	-	
Myrsine australis	-	-		0.65	0.46		-	-	
Pennantia corymbosa	4.80	0.31	0.14	6.18	0.08	0.09	<0.01	0.96	
Pittosporum tenuifolium	7.25	0.25	0.21	4.91	0.52	0.25	1.15	0.38	
Pseudopanax arboreus	**42.34**	**<0.01**	**0.33**	**22.08**	**<0.01**	**0.15**	3.10	0.21	0.05
Pseudopanax crassifolius	**31.92**	**<0.01**	**0.28**	**30.20**	**<0.01**	**0.21**	**9.48**	**0.05**	**0.13**
Raukaua edgerleyi	0.01	0.92		0.50	0.49		2.97	0.12	
Pseudowintera colorata	-	-		-	-		0.40	0.53	
Quintinia serrata	<0.01	0.94		-	-		-	-	
Schefflera digitata	-	-		2.86	0.15		0.28	0.60	
Weinmannia racemosa	**12.10**	**<0.01**	**0.11**	**9.24**	**<0.01**	**0.06**	6.00	0.11	0.11

The main canopy tree species showed different unimodal probabilities of occurrence in different social classes (Figure 71). The species with the highest probabilities of occurrence in social class 3 were *B. tawa* with a modelled maximum of 71.1 % (± 6.2) at a gap size of 688 m², *P. ferruginea* with 68.8 % (± 6.2) at a gap size of 887 m², *D. cupressinum* with 63.4 % (± 11.1) at 1212 m² and *E. dentatus* with 61.1 % (± 6.9) at 774 m². All other main canopy tree

species were scarce, with *P. taxifolia* showing a maximum of 27.2 % (± 14.2) at a gap size of 1249 m², *P. totara* with 13.6 % (± 7.3) at 1000 m² and *D. dacrydioides* with 11.2 % (7.7) at 997 m².

In social class 4, the probabilities of occurrence increased for *B. tawa* to a maximum of 86.9 % (± 4.3) at a gap size of 579 m² and for *E. dentatus* to 74.3 % (± 5.9) at a gap size of 714 m². They decreased slightly for *P. ferruginea* to a maximum of 67.5 % (± 6.3) at 815 m², for *D. cupressinum* to 60.3 % (± 6.6) at 960 m² and for *P. taxifolia* to 21.1 % (± 12.0) at 1249 m². Trees of *K. excelsa* (14.5 % ± 14.1 at 36 m²), *P. totara* (8.9 % ± 6.0 at 1192 m²), *D. dacrydioides* (6.3 % ± 3.8 at 826 m²) and *P. trichomanoides* (5.5 % ± 3.1 at 416 m²) were scarce in this social class.

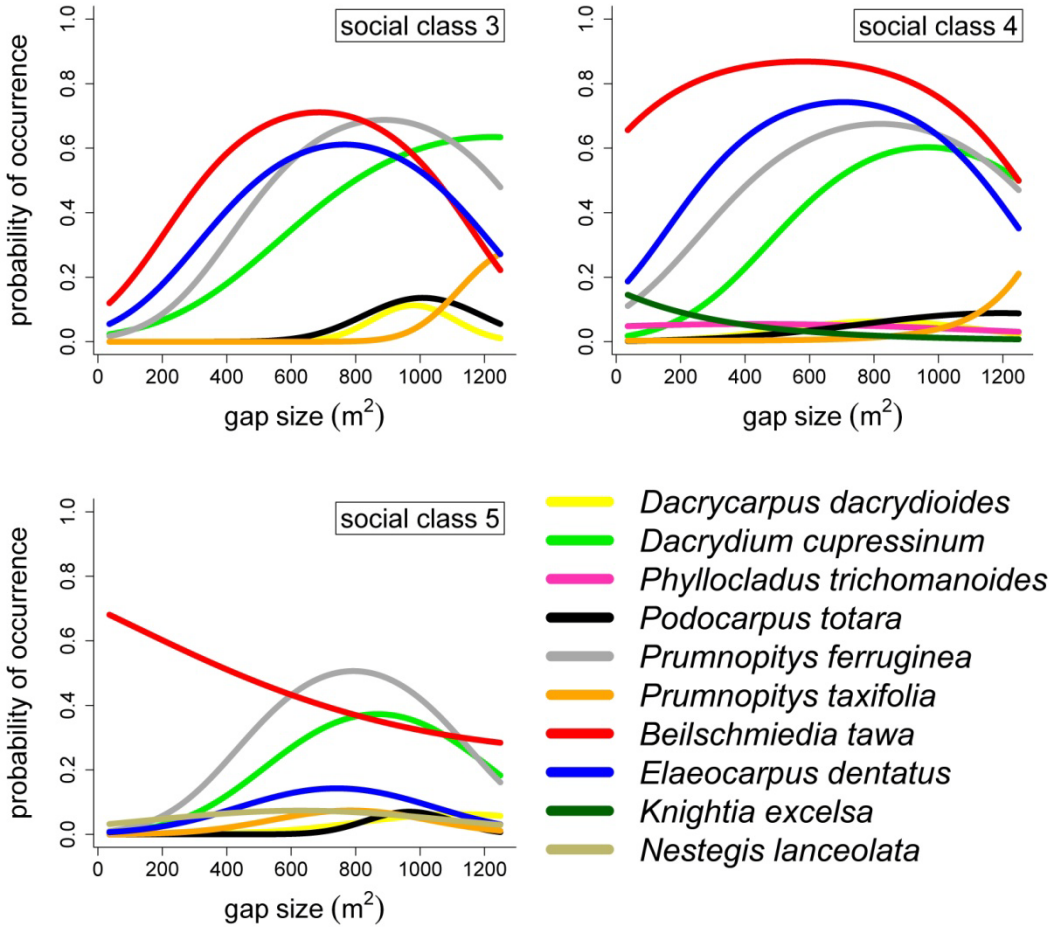

Figure 71. Probability of occurrence of large tree species of 3 different social classes in different gap sizes

The probability of occurrence decreased further for trees of social class 5 with *B. tawa* having the maximum occurrence (68.1 % ± 14.2) at the smallest gap size (36 m²). *Prumnopitys ferruginea* (50.6 % ± 7.4) and *D. cupressinum* (37.3 % ± 7.3) did also occur in fewer gaps. The gap size where the probability of occurrence peaked also decreases to 787 m² for *P. ferruginea* and 867 m² for *D. cupressinum*. All other tree species became scarce. In particular, *E. dentatus* decreased to 14.3 % (± 5.5) of the gaps at a gap size of 741 m². *Prumnopitys taxifolia* (7.4 % ± 4.3 at 787 m²), *P. totara* (7.0 % ± 6.0 at 960 m²), *N. lanceolata* (7.3 % ± 3.9 at 632 m²) and *D. dacrydioides* (6.3 % ± 4.3 at 1113 m²) were scarce in social class 5.

The subcanopy tree species showed again a very different relationship between the presence of trees and gap size for different social classes (Figure 72).

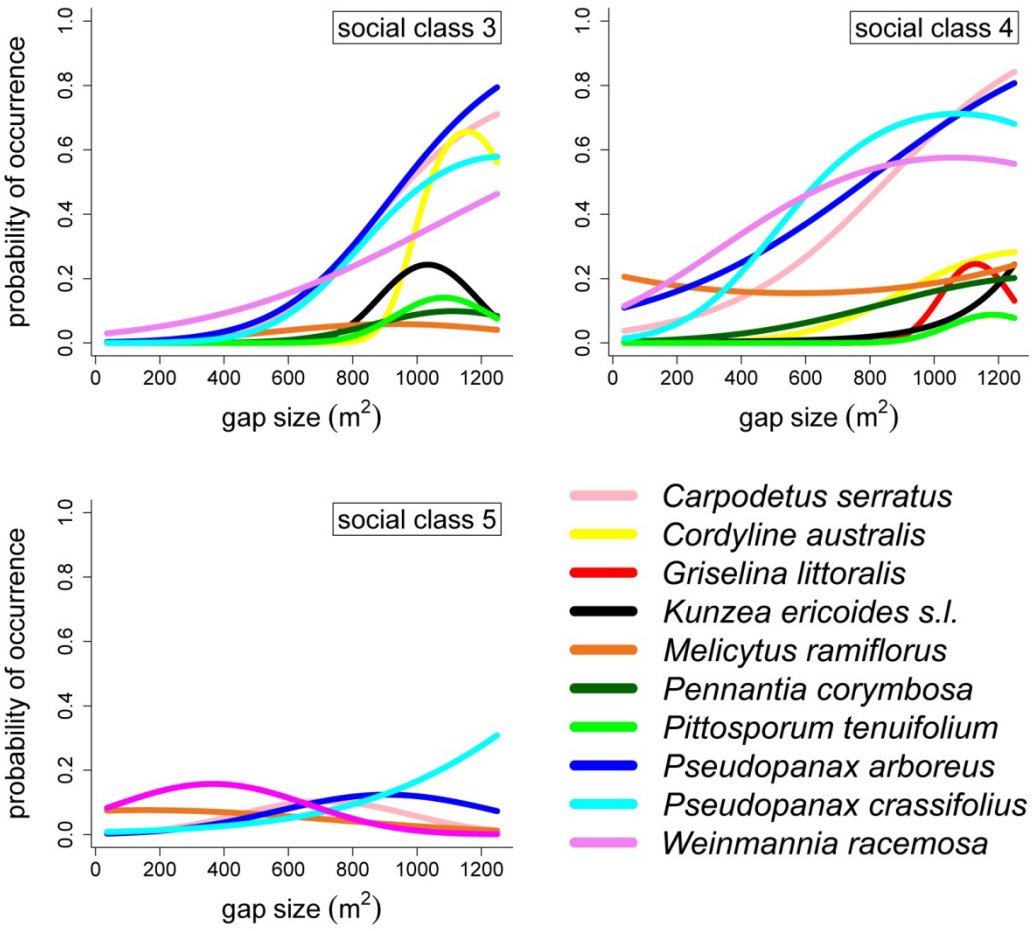

Figure 72. Probability of occurrence of small tree species of 3 different social classes in different gap sizes

All subcanopy tree species of social class 3 were absent or at least rare in smaller gaps. The only species occurring in gaps < 400 m² was *W. racemosa*. The highest probability of occurrence correlated for several species with that largest gaps, in particular *P. arboreus* with 79.4 % (± 10.2) at 1249 m², *C. serratus* with 71.1 % (± 12.0) at 1249 m², *P. crassifolius* with 57.8 % (± 13.5) at 1249 m² and *W. racemosa* with 46.3 % (± 12.9) at 1249 m². The light-demanding species *C. australis* showed a maximum probability of 65.6 % (± 10.8) at 1152 m². In larger gaps, its presence declined again. *Kunzea ericoides s.l.*, another light-demanding tree species, also had its maximum probability of occurrence in very large gaps (24.3 % ± 10.3 at 1033 m²). The other tree species were rather rare, even though they also showed their highest probability of occurrence in large gaps with a maximum of 14.1 % (± 8.3) for *P. tenuifolium* in gaps of 1083 m² and 9.9 % (± 5.6) for *P. corymbosa* at 1113 m². The unimodal distribution of *M. ramiflorus* was quite level and peaked at only 5.9 % (± 3.5) probability at a gap size of 926 m².

These relationships were similar for trees of social class 4, in particular for *C. serratus* (84.2 % ± 8.5 at 1249 m²), *P. arboreus* (80.7 % ± 9.3 at 1249 m²), *P. crassifolius* (71.2 % ± 6.5 at 1078 m²) and *W. racemosa* (57.6 % ± 7.0 at 1049 m²). But here, these tree species started to occur in much smaller gaps. Light-demanding *C. australis* occurred far less in social class 4 than in class 3 and its probability of occurrence peaked at only 28.2 % (± 12.6) in gaps of 1249 m². *Pennantia corymbosa* doubled to 20.2 % (± 10.7) in the largest gaps of 1249 m², while all other tree species decreased in their occurrence. *Kunzea ericoides s.l.* (24.3 % ± 12.5) and *M. ramiflorus* (24.2 % ± 10.8) had their largest probability of occurrence at a gap size of 1249 m² but while *K. ericoides s.l.* was restricted to the largest gaps, *M. ramiflorus* was found in all gaps sizes. *Griselinia littoralis* was only found in this social class only in very large gaps with a maximum probability of 24.5 % (± 11.9) at 1135 m² gap size. The rarest species in this class was light-demanding *P. tenuifolium* with a maximum of only 8.7 % (± 6.8) at gaps of 1192 m².

Only 5 species of subcanopy trees were found in the understorey of gaps and even there they occurred only infrequently. Of those, *P. crassifolius* showed its highest probability of occurrence of 30.8 % (± 12.6) in the largest gaps of 1249 m², while no significant

relationships were found for *C. serratus* (10.3 % ± 4.9 at 714 m²), *M. ramiflorus* (7.6 % ± 5.9 at 161 m²), *P. arboreus* (12.4 % ± 5.0 at 910 m²) and *W. racemosa* (15.7 % ± 6.2 at 372 m²).

4.3.4. Species abundances

Modelling of the relationship between the absolute abundance of trees and gap size was carried out for 10 major canopy species and was significant ($p<0.05$) for all tree species except *P. trichomanoides* (max = 2.4 trees ± 1.51 at 1249 m²), *K. excelsa* (max = 3.4 trees ± 1.57 at <10 m²) and *N. lanceolata* (max = 3.5 trees ± 0.94 at 1249 m²) (Figure 73). The abundance of trees in small gaps <200 m² was extremely low, with less than 5 trees of any species. The only exception was *B. tawa* where the modelled abundance even in the smallest gaps was close to 20 trees. Its maximum of 23.0 trees (± 0.69) was found in gaps of 463 m². The tree species with the overall highest abundance was *D. cupressinum* with a maximum of 28.0 trees (± 1.09) at a gap size of 963 m². In the smallest gap size, the abundance of *D. cupressinum* was close to zero, but increased almost proportionally to gap size after that. At a gap size of 300 m², its abundance began to increase faster than gap size. The relationship was similar and also close to proportional for *P. ferruginea* with a maximum of 20.7 trees (± 0.80) at a gap size of 852 m². After reaching the maximum abundance, larger gap sizes lead to a strong decline in abundances of both species. At a gap size of 710 m², the modelled abundances of *D. cupressinum* and *B. tawa* were equal and at a gap size of 820 m² they were equal for *P. ferruginea* and *B. tawa*.

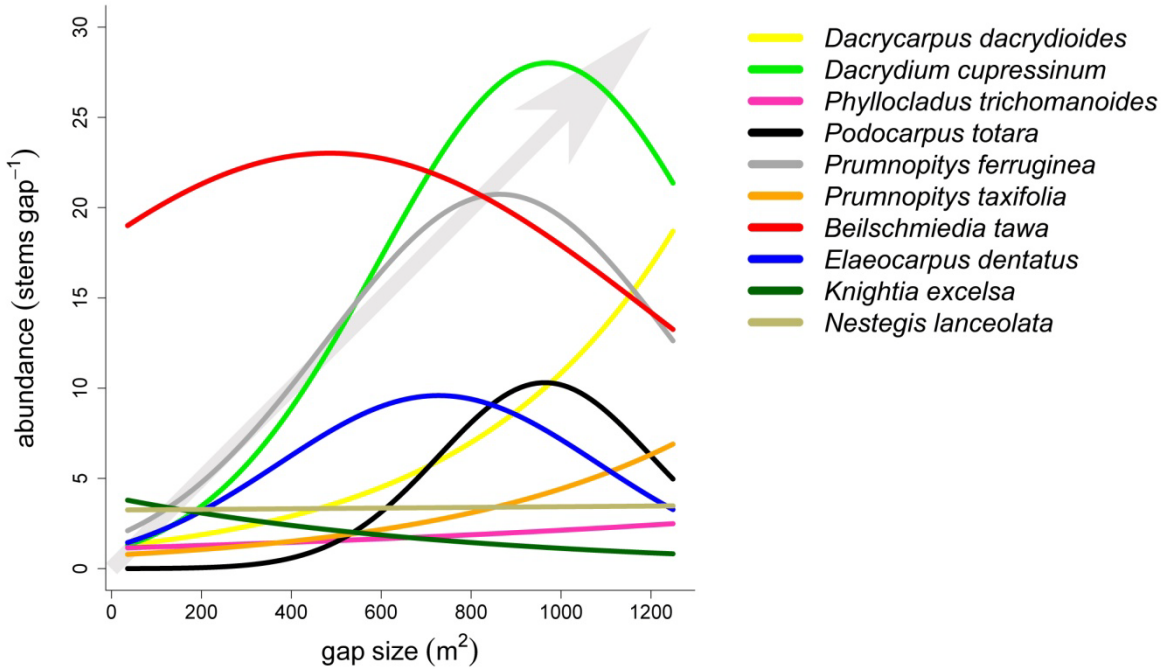

Figure 73. Modelled relationship between abundance of 10 major canopy tree species and gap size; the large grey arrow indicates the slope of a proportional relationship with the basis 5 trees at 200 m²

The abundance of *D. dacrydioides* showed a strong correlation with gap size. It was very low up to a gap size of 600 m², but increased after that significantly to a maximum of 15 trees (± 4.38) in the largest gap size of 1249 m². All other main canopy tree species were less abundant, with *E. dentatus* (9.6 trees ± 0.52 in gaps of 713 m²) and *P. totara* (10.3 trees ± 1.85 in gaps of 956 m²) being the only other species in substantial numbers that showed a unimodal distribution. *Prumnopitys taxifolia* was the last of the main canopy species to show a strong positive correlation between abundance and gap size, with a maximum of 6.9 trees (± 1.23) at a gap size of 1249 m². Even though these relationships were all significant, the spread in the data was large and other factors can be expected to also have a large effect on species abundance.

The relationship between species abundance of 9 subcanopy tree species and gap size was significant for all species except *M. ramiflorus* (max = 3.5 trees ± 0.72 at 1249 m²), *P. corymbosa* (max = 5.8 trees ± 1.16 at 1249 m²) and *P. tenuifolium* (max = 2.9 trees ± 1.11 at 1249 m²). The only species with a unimodal relationship was *C. serratus* with 15.2 trees (± 0.90) at a gap size of 958 m² (Figure 74). All other subcanopy species had their maximum abundance in the largest gap size with *P. arboreus* (max = 25.5 trees ± 1.27 at 1249 m²)

having the overall largest abundance, followed by *P. crassifolius* (max = 17.4 trees ± 1.32 at 1249 m²).

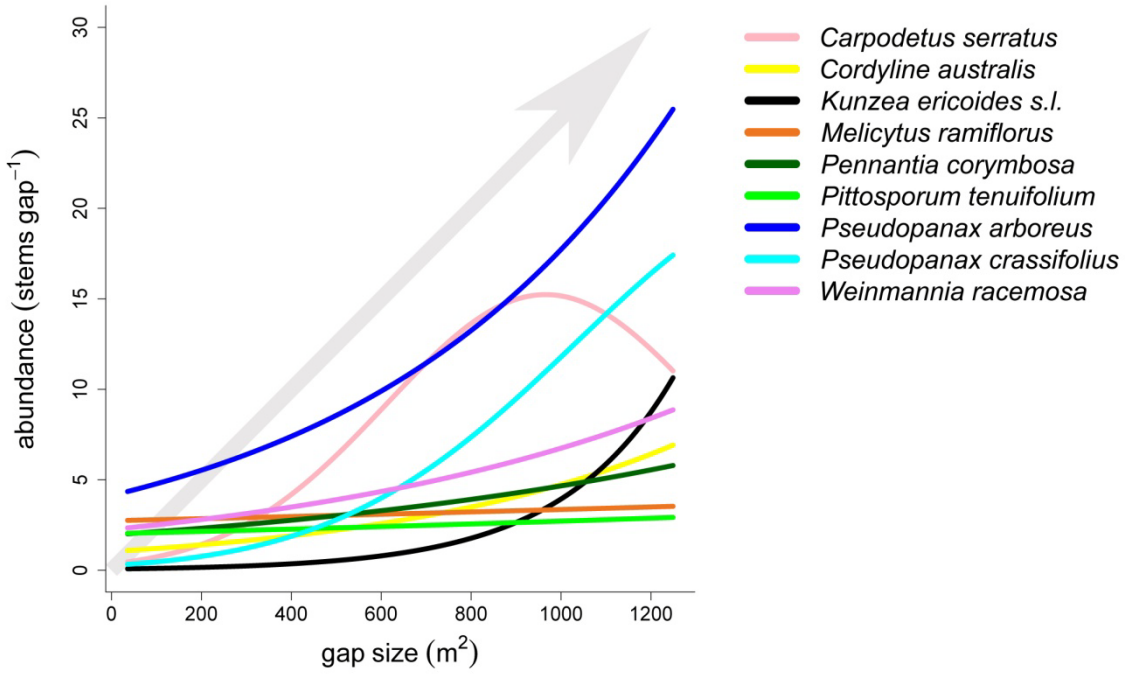

Figure 74. Modelled relationship between abundance of 9 smaller tree species and gap size; the large grey arrow indicates the slope of a proportional relationship with 5 trees in gaps of 200 m²

Kunzea ericoides s.l. was rare in gaps smaller than 800 m² but abundances increased significantly after that to 10.6 trees (± 1.65) at a gap size of 1249 m². *Cordyline australis* (max = 6.9 trees ± 0.89 at 1249 m²) and *W. racemosa* (max = 8.9 trees ± 0.77 at 1249 m²) showed a slow but steady increase in abundances up to the maximum gap size of 1249 m².

Among the tree ferns, *D. squarrosa* was the most abundant species (max = 45.1 trees ± 1.28 at 1104 m²), showing a significant proportional relationship between tree abundance and gap size (Figure 75). The relationship was not significant for *C. dealbata* (max = 2.1 trees ± 1.90 at 1249 m²), the least abundant of the tree ferns. *Cyathea smithii* showed a significant unimodal relationship with a maximum of 9.1 trees at a gap size of 649 m², while *D. fibrosa* was most abundant in the largest gap size (max = 5.1 trees ± 0.64 at 1249 m²).

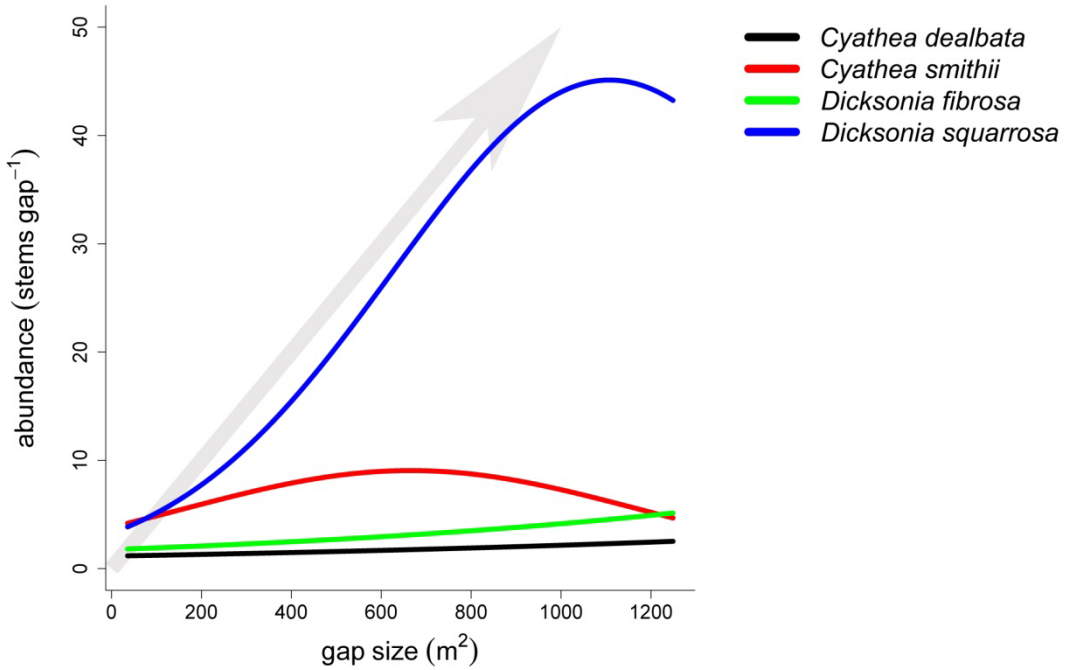

Figure 75. Modelled relationship between abundance of 4 tree fern species and gap size; the large grey arrow indicates the slope of a proportional relationship with 10 trees in gaps of 200 m²

The above analyses do not take social status into account. The mere presence of a tree species in a gap does not necessarily mean that this species is likely to be successful in the long term. Therefore, the relationship between tree abundance and gap size was also analysed separately for the 7 most abundant tree species in the highest social class that occurred in gaps: codominant social class 3 trees (Figure 76).

The number of social class 3 trees increased with gap size for all species of interest. Among them, *P. arboreus* showed the strongest relationship between tree abundance and gap size and had the highest abundance with a maximum of 12.2 trees (± 1.00) at the largest gap size of 1249 m². The only other species that showed the highest abundance in the largest gap size was *W. racemosa* (max = 6.0 trees ± 0.85 at 1249 m²). But apart from those two species, all other species showed unimodal distributions. While *B. tawa* was most abundant species in smaller gaps with a maximum abundance in medium-sized gaps (max = 4.3 trees ± 0.37 at 700 m²), all other tree species were scarce in small gaps and had their highest abundance in large gaps. Of those, *D. cupressinum* was the most abundant podocarp with 10.1 trees (± 0.67) at a gap size of 1070 m², followed by *P. ferruginea* with 6.5 trees (± 0.51) at a 962 m².

Elaeocarpus dentatus (max = 4.8 trees ± 0.43 at 827 m²) showed a maximum abundance similar to *B. tawa*, even though assigned to larger gaps. *Pseudopanax crassifolius* trees of social class 3 (max = 6.1 trees ± 0.68 at 1114 m²) showed the lowest abundance of all tree species in gaps below 750 m², but increased significantly in abundance with gap size.

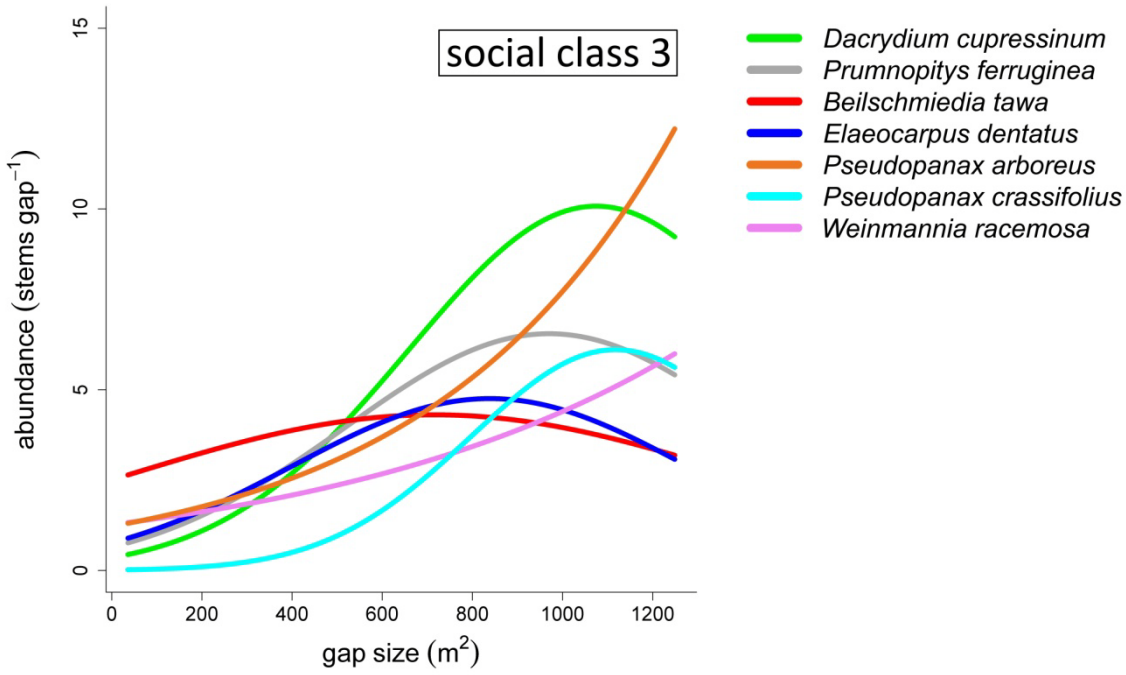

Figure 76. Modelled relationship between abundance of 7 tree species of social class 3 and gap size

4.3.5. Age structure

The age of 359 trees in harvesting gaps out of a total of 372 cored trees could be estimated for this part of the study, while 13 tree cores were either incomplete or missed the pith of the tree considerably. The age of the analysed trees ranged from 27 to 133 years. Comparing the years of establishment of 8 tree species shows that successful recruitment was not evenly distributed throughout time (Figure 77). Instead, there were phases where recruitment was successful and phases where successful recruitment was scarce. One such phase of successful recruitment that stands out occurred c. 1935/40 and involved mainly *P. ferruginea*, *E. dentatus* and *D. cupressinum*, but to some degree also *P. trichomanoides*.

Prumnopitys ferruginea and *E. dentatus* were found to have established continuously in the forest before 1935/40, but showed a significant increase at that time. This effect was strongest for *E. dentatus*, where recruitment increased by a factor of 10. While *B. tawa* also showed continuous recruitment in the decades prior to this event, no trees successfully established in the 15 years that followed this overall increase in 1935/40. This strong decline in recruitment was observed for all species. But it was also observed that *P. taxifolia* and *D. dacrydioides* established in those years, for the first time in over half a century.

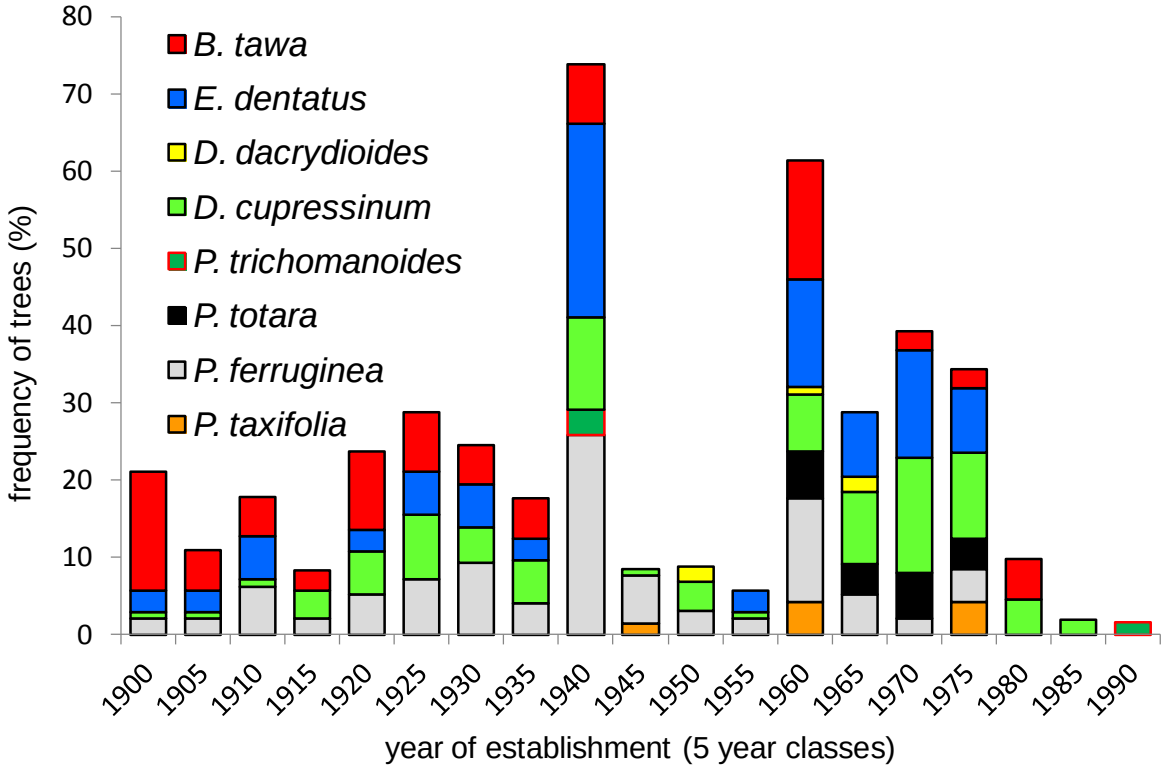

Figure 77. Times of establishment of trees in gaps of different sizes in the Māori blocks; class names are the upper limits of classes; relative frequencies are individual class values for each species

Another period of successful recruitment occurred in 1955/60. Even though recruitment of *P. ferruginea*, *D. cupressinum* and *E. dentatus* was not as strong as it was in 1935/40, there was also successful recruitment of *D. dacrydioides*, *P. totara* and *P. taxifolia*. In contrast to the extremely low numbers of trees that got established after 1940, the boost of recruitment in 1955/60 continued for the next decades in *D. cupressinum*, *E. dentatus* and *P. totara* and to a smaller extend also in *P. taxifolia* and *D. dacrydioides*. The small numbers of

observations after 1975 are due to the small diameters of those trees, as they were impracticable to core.

Due to the overall small numbers of trees of *D. dacrydioides*, *P. trichomanoides*, *P. totara* and *P. taxifolia*, modelling the relationship between tree age and gap size could only be carried out for 330 trees of *D. cupressinum*, *P. ferruginea*, *B. tawa* and *E. dentatus*. Mixed-effect models that included the sampling plot as a random effect showed negative relationships between age of trees and the size of gaps that were created 56 years ago, with trees in larger gaps being generally younger than trees in smaller gaps (Table 42). These relationships were significant for *D. cupressinum* ($F_{(1,36)}$ = 9.84) and *E. dentatus* ($F_{(1,31)}$ = 4.10) but not for *P. ferruginea* ($F_{(1,44)}$ = 1.19) and *B. tawa* ($F_{(1,38)}$ = 1.22).

Table 42. Relationship between the age of trees and gap size for 4 tree species 56 years after gap creation; Mean age$_{50}$ = mean age in a gap size of 50 m²; Mean age$_{1249}$ = mean age in a gap size of 1249 m²

species	Mean age$_{50}$	Mean age$_{1249}$	*n*	p	F
D. cupressinum	90.9	49.2	119	<0.01	9.84
P. ferruginea	78.1	68.3	108	0.28	1.19
B. tawa	102.1	84.9	58	0.28	1.22
E. dentatus	91.3	58.6	45	0.05	4.10

The other podocarps occurred mainly in large gaps with their ages ranging in case of *D. dacrydioides* from 48 to 67 years (μ = 57 years ± 3.9), in case of *P. trichomanoides* from 27 to 85 years (μ = 72 years ± 9.1), *P. totara* from 40 to 51 years (μ = 47 years ± 1.3) and *P. taxifolia* from 38 to 70 years (μ = 51 years ± 4.7).

4.3.6. Diameter growth

Due to the low numbers of *D. dacrydioides*, *P. trichomanoides*, *P. totara* and *P. taxifolia*, the relationship between periodic mean annual increment (*mai*) and gap size could only be modelled for 467 trees of *D. cupressinum*, *P. ferruginea*, *B. tawa* and *E. dentatus*. All trees showed a positive correlation between the periodic mean annual diameter increment (*mai*) over a period of 52 years and gap size in case of all tree species (Table 43). This relationship was significant for all trees of social class 3 but strongest for *D. cupressinum*. With gap size

increasing from 50 m² to 1249 m², the mean annual diameter increment of social class 3 trees of *D. cupressinum* increased by 102.9 %.

Table 43. Relationship between radial mean annual diameter increment (*mai*) and gap size for 4 tree species of social classes 3 and 4 within a period of 52 years; mai_{50} = mean annual increment (mm) in a gap size of 50 m²; mai_{1249} = mean annual increment (mm) in a gap size of 1249 m²; random effect in class 3 (SD intercept = 0.51; residuals = 0.89); random effect in class 4 (SD intercept = 0.34; residuals = 0.52)

Species	Intercept	slope	SE_{inter}	SE_{slope}	mai_{50}	mai_{1249}	*n*	p
Social class 3								
D. cupressinum	2.22	0.001993	0.41	0.0004342	2.32	4.71	110	<0.01
P. ferruginea	2.56	0.001294	0.38	0.0004342	2.62	4.18	101	<0.01
B. tawa	2.67	0.001037	0.35	0.0004579	2.73	3.97	55	0.02
E. dentatus	3.33	0.001239	0.36	0.0004598	3.39	4.88	64	<0.01
Social class 4								
D. cupressinum	1.53	0.001403	0.47	0.0006023	1.60	3.28	29	0.02
P. ferruginea	2.08	0.000684	0.23	0.0003063	2.12	2.94	56	0.02
B. tawa	2.31	0.000089	0.26	0.0003229	2.31	2.42	38	0.78
E. dentatus	2.94	0.000041	0.41	0.0005531	2.94	2.99	14	0.94

The relationship was not nearly as strong for *P. ferruginea* with an increase of 59.1 % and the angiosperms *B. tawa* (45.6 %) and *E. dentatus* (43.8 %). Social class 4 trees were generally growing slower and only the podocarps showed a significant correlation with an increase of 104.9 % for *D. cupressinum* and 38.8 % for *P. ferruginea*, while the angiosperm *B. tawa* increased by only 4.6 % and *E. dentatus* by only 1.7 %.

The overall fastest growing tree species was *E. dentatus*. Only in the largest gaps, social class 4 trees of *D. cupressinum* had a larger mean diameter growth than social class 4 trees of *E. dentatus* (Figure 78). *Beilschmiedia tawa* of social class 3 was growing faster than *D. cupressinum* and *P. ferruginea* only in small gaps up to around 450 m². At this stage *D. cupressinum* and *P. ferruginea* surpassed *B. tawa*. In particular *D. cupressinum* was now growing much faster not only than *B. tawa* but also than *P. ferruginea* (Figure 79). In social class 4, all four trees species apart from *B. tawa* were growing much slower than in class 3 and no relationship was detected between diameter growth and gap size for *B. tawa* and *E. dentatus*.

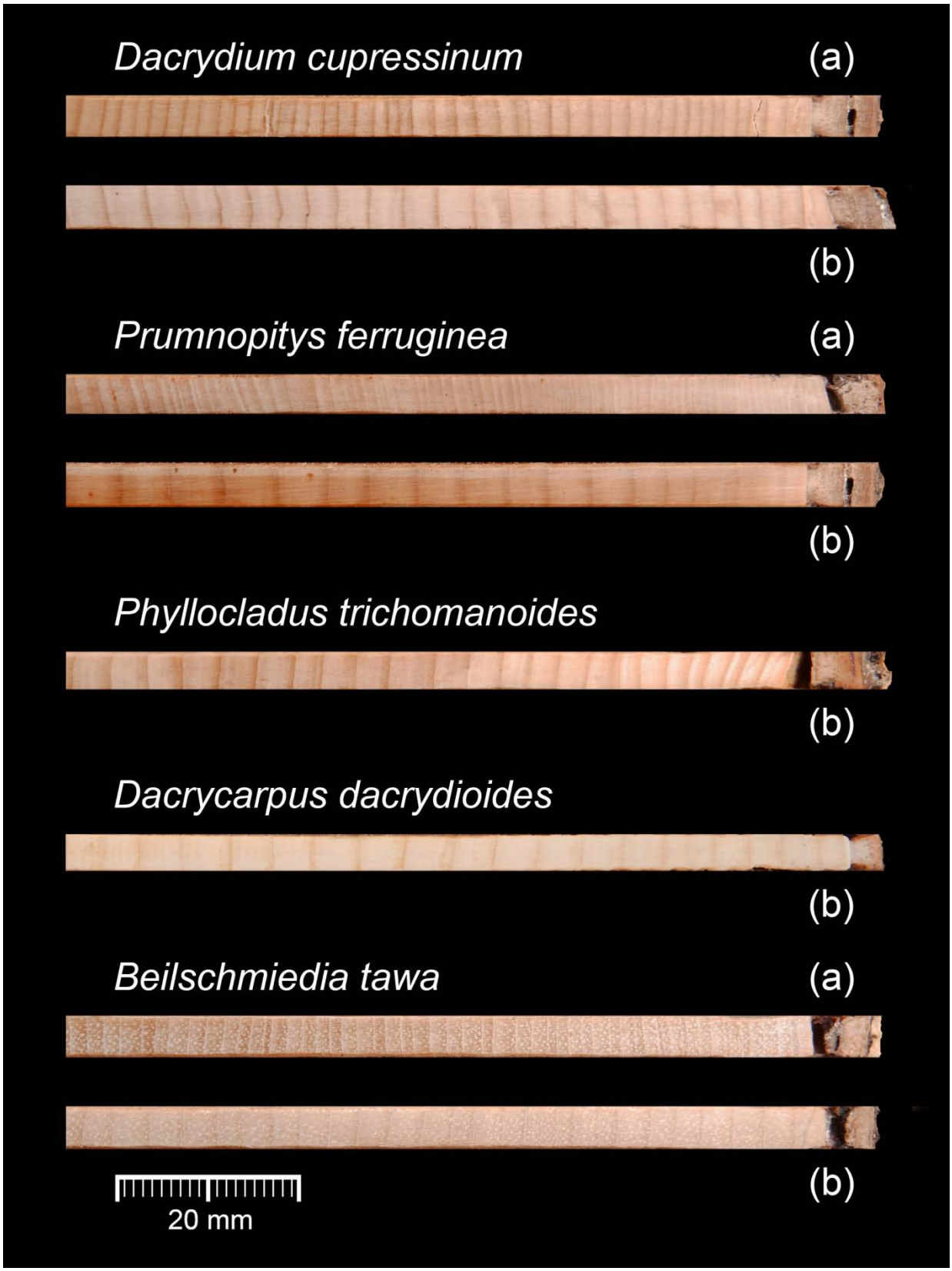

Figure 78. Difference between slow and fast growth of 4 different tree species highlighting the growth range of those species, where (a) shows tree cores taken in small gaps <400 m² and (b) shows tree cores taken in large gaps >1000 m²

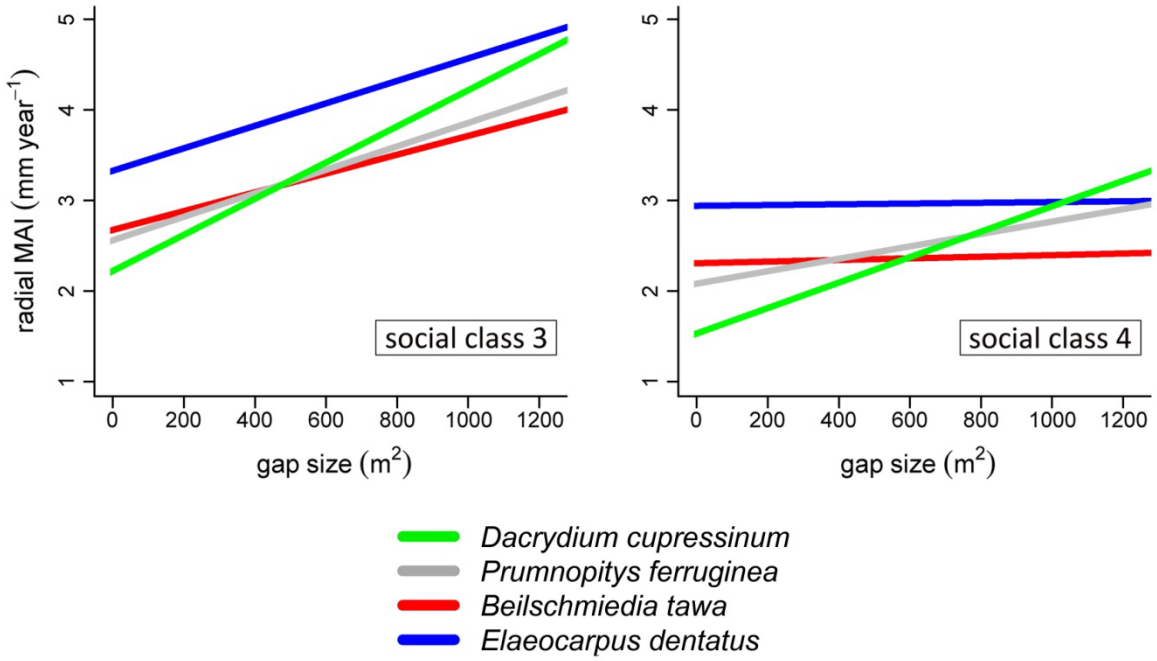

Figure 79. Relationship between mean annual diameter increment (*mai*) over a period of 52 years and gap size of four main canopy species of social classes 3 and 4

At a gap size of 350 m², *P. ferruginea* was surpassing *B. tawa* in diameter growth but was never growing faster than *E. dentatus*. *Dacrydium cupressinum* on the other hand, even though it was the slowest growing species in smaller gaps, surpassed *B. tawa* in gaps of 580 m², *P. ferruginea* in gaps of 750 m² and *E. dentatus* in gaps larger than 1025 m². Sample sizes for the other podocarps were too low for reliable statistical modelling, but periodic annual mean increments in social class 3 ranged for *D. dacrydioides* from 3.38 to 5.68 mm yr^{-1} (μ = 4.35 mm ± 0.27), for *P. trichomanoides* from 1.95 to 4.41 mm yr^{-1} (μ = 3.49 mm ± 0.56), for *P. totara* from 2.87 to 7.03 mm yr^{-1} (μ = 4.44 mm ± 0.48) and for *P. taxifolia* from 3.16 to 7.42 mm yr^{-1} (μ = 5.83 mm ± 0.78). In social class 4, the diameter increment was much lower with 1.91 to 3.50 mm yr^{-1} (μ = 2.91 mm ± 0.35) for *P. totara* and 2.44 to 3.63 mm yr^{-1} (μ = 3.04 mm ± 0.60) for *P. taxifolia*.

4.3.7. Growth release and suppression

Changepoint analysis could be carried out for 304 cored trees in different size harvesting gaps in the Māori blocks and showed that phases of growth release and suppression are common features in all tree species of interest. But beside those general phases that

affected only individual trees or small groups, there were also phases that affected trees on a larger scale. Two of those phases of release affecting trees on a larger spatial scale correlate with a devastating cyclone that hit the North Island in 1936 and high-grading of the Māori blocks in 1956/58 (Figure 80).

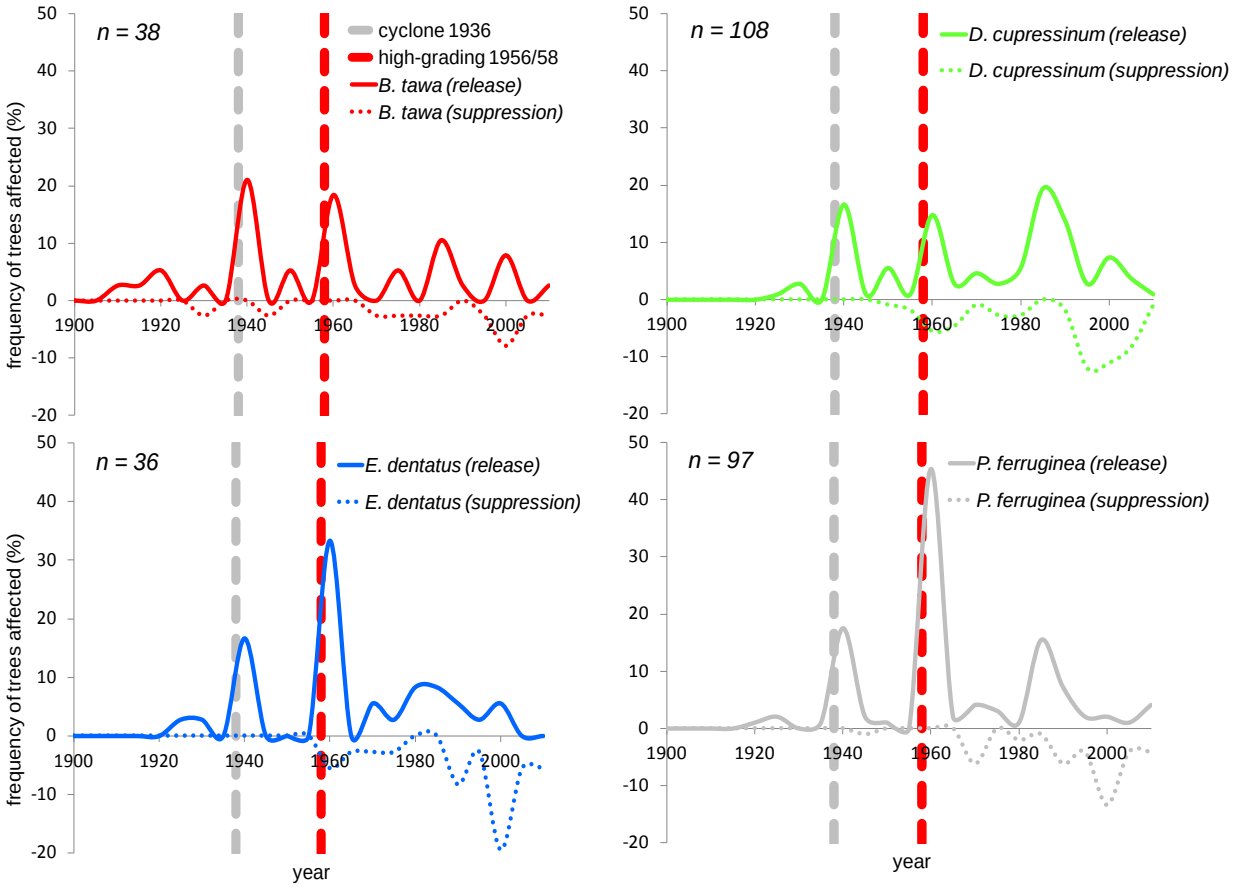

Figure 80. Times of abrupt changes in growth of abundant canopy species, where positive values show phases of release and negative values show phases of suppression; the grey vertical dashed line indicates the time of the devastating cyclone in 1936 and the red vertical dashed line indicates the time of high-grading the Māori blocks in 1956/58

Trees that were present in 1936 and are found in gaps today were seedlings at that time, with mean diameters of 3.9 cm (± 0.2) for *B. tawa*, 2.5 cm (± 0.5) for *E. dentatus*, 2.5 cm (± 0.3) for *D. cupressinum* and 2.2 cm (± 0.2) for *P. ferruginea*. While the cyclone of 1936 released the growth of all species of interest, it seemed to have been most important for *D. cupressinum*. All *D. cupressinum* trees that are found in gaps today were seedlings of up to 25 years of age at that time. They showed suppressed growth, suggesting sub-optimal growing conditions in a low-light environment and had diameters of 0.4-5.7 cm (μ = 2.2 cm ± 0.2) in 1936. The change in growth conditions allowed them to proceed quickly into larger

size classes. When high-grading was carried out in the Māori blocks in 1956/58, these trees were already advanced saplings and small pole trees up to 45 years old with a mean diameter of 8.0 cm (± 0.5) and a range of 2.9-14.4 cm. This means that they increased on average 5.7 cm in diameter in those 20 years. But these values include all social classes of trees, with trees of higher social classes growing faster than dominated trees of lower social classes.

While the cyclone of 1936 affected similar numbers of trees of *B. tawa* (21 %), *E. dentatus* (17 %), *D. cupressinum* (17 %) and *P. ferruginea* (18 %), this was different after high-grading in 1956/58. The effect was much stronger for *P. ferruginea* (45 %) and *E. dentatus* (33 %), but slightly lower for *D. cupressinum* (15 %) and *B. tawa* (18 %) (Figure 81). Of the trees that had shown a release after the cyclone of 1936, 35 % showed a second release after high-grading in 1956/58.

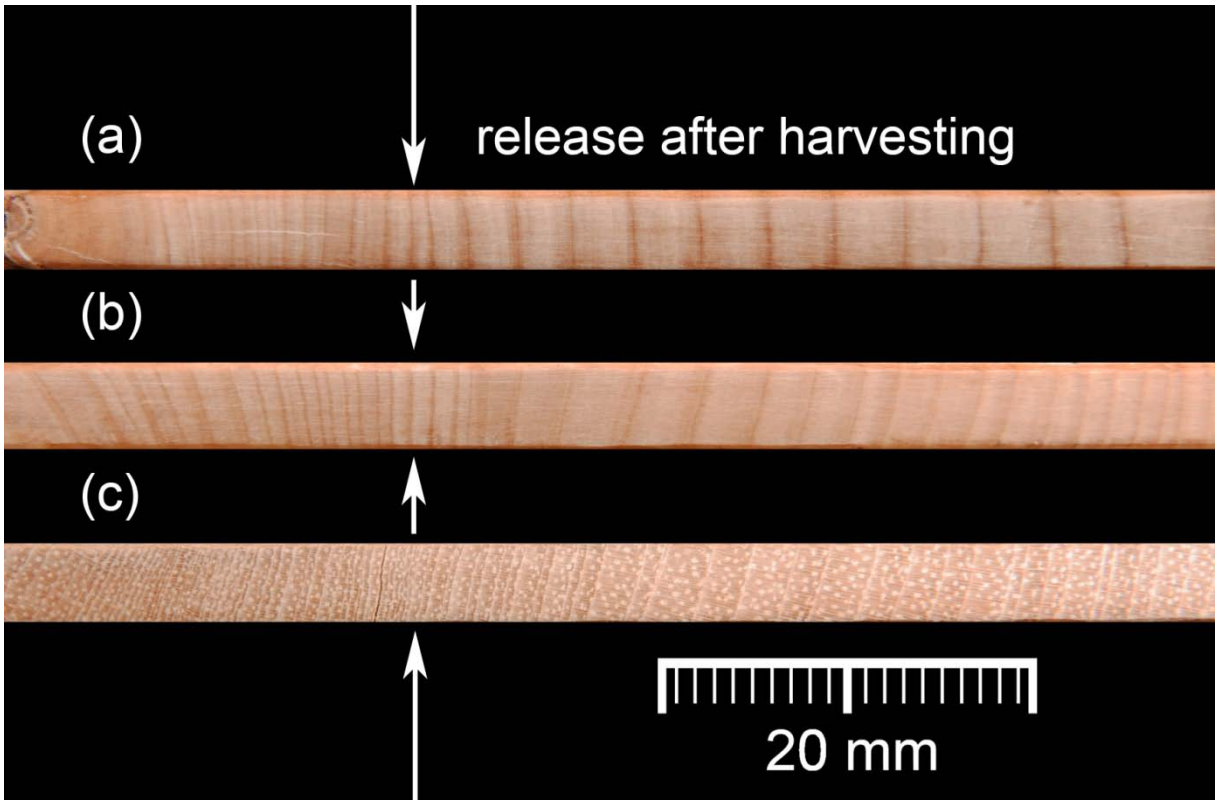

Figure 81. Growth release after harvesting in 1956/58 visible in (a) *D. cupressinum*, (b) *P. ferruginea* and (c) *B. tawa*

A third phase of growth release that affected all species of interest can be observed between 1985 and 1990, 30 years after high-grading. This coincides with the destructive cyclone Bola that hit the North Island in March 1988, one of the most devastating cyclones in recent New Zealand history (Marden & Rowan, 1993). At that time, trees of *D. cupressinum* that were seedlings at the time of the cyclone of 1936 had grown in diameter, between 1958 and 1988, by another 2.5-21 cm (μ = 11.4 cm ± 0.7) to 8.5-33.2 cm (μ = 19.3 cm ± 1.0), becoming large pole trees at the time of cyclone Bola. Of all trees that were released from competition at the time of high-grading, 25 % showed a second release in 1988. But no tree that was released in 1936 and 1956/58 showed a third release in 1988.

Trees were found to not only share phases of growth release but also phases of slow growth. Even though these phases were not as common as release, such a phase of extremely slow growth that affected *B. tawa* (8 %), *E. dentatus* (19 %), *D. cupressinum* (12 %) and *P. ferruginea* (13 %) was found to begin around 1995-2000. Interesting to note is that of all trees that showed a growth release at the time of the cyclone of 1936 as well as after high-grading, 33 % showed this very slow growth that began around 1995-2000 and is still continuing.

Only small numbers of observations were available for *D. dacrydioides*, *P. taxifolia*, *P. totara* and *P. trichomanoides*. Nevertheless, they show similar patterns of growth release to the more abundant species (Figure 82). But while only *D. dacrydioides* and *P. trichomanoides* showed a growth release after high-grading in 1956/58, all four species show an increase in releases at the time of the cyclone Bola. No phases of suppression were observed for those tree species.

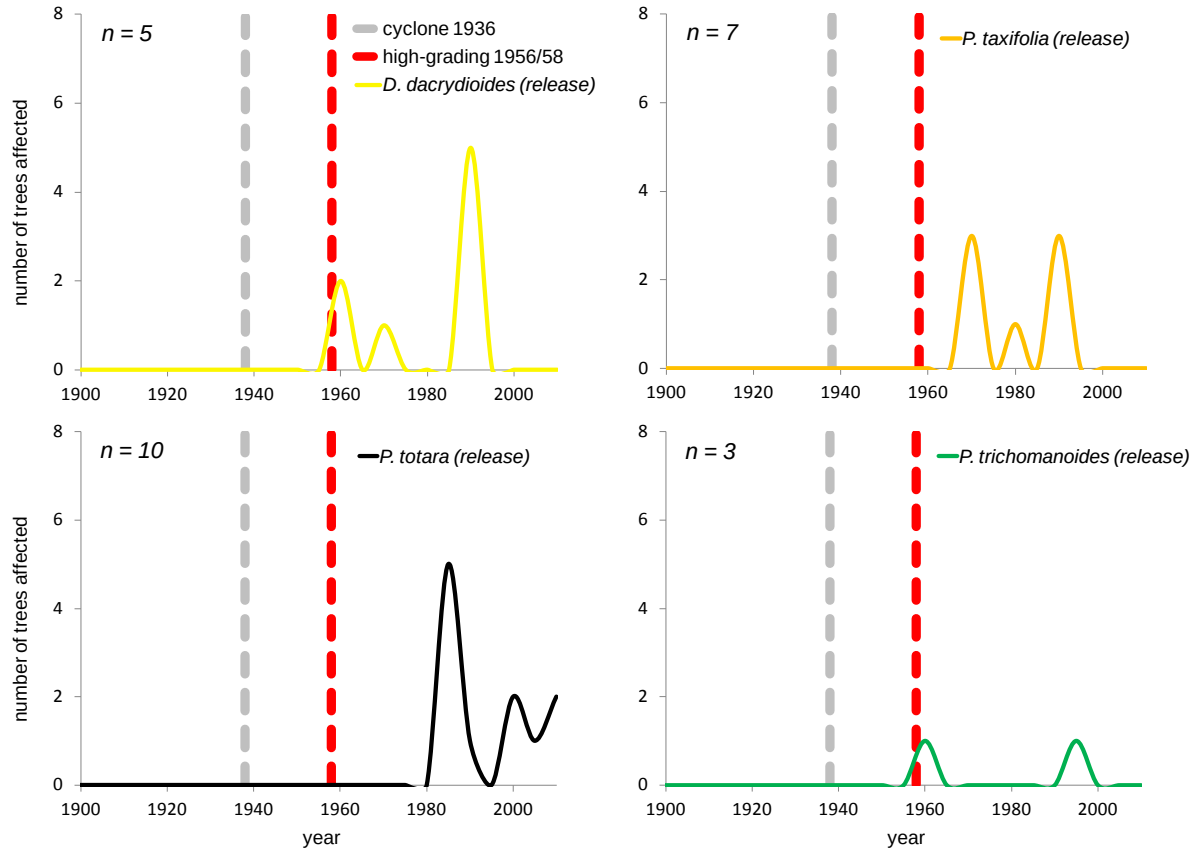

Figure 82. Times of abrupt changes in growth of rare canopy species, where positive values show phases of release; the grey vertical dashed line indicates the time of the devastating cyclone in 1936 and the red vertical dashed line indicates high-grading in 1956/58

4.4. Discussion

4.4.1. Harvesting

Harvesting inventories that are based on stump counts and measurements are generally related to stump extraction for bioenergy or forest health (Berch et al., 2012). This seems to be the first time that such an inventory was carried out to investigate pre-harvesting conditions in form of frequency, abundance and dimensions of stumps of harvested trees 56 years after harvesting. Results showed that it can be a suitable method to investigate past distributions of emergent podocarps in podocarp-broadleaved forest. Advanced decay of stumps, however, made the accurate estimation of dbh (diameter at breast height = 1.4 m) based on dsh (diameter at stump height = 0.3 m above ground) measurements difficult, but grouping the stumps into 20 cm diameter classes reduced this problem.

The inventory showed similar pre-harvesting densities of large podocarps in the old-growth forest, the FRI blocks and the high-graded Māori blocks, providing evidence that all blocks belonged to a forest type generally described as medium-density podocarp-broadleaved forest (M2) with 20-50 merchantable podocarps per hectare and a merchantable volume of 100-300 m^3 ha^{-1} (Beveridge, 1983; McKelvey & J. L. Nicholls, 1957). In the old-growth forest and the selective harvesting blocks, those trees were all emergent above a dense canopy of *B. tawa*, and it is likely that this was also the case in the high-graded Māori blocks.

Differences between the blocks still occurred in the larger diameter classes. But due to the infrequent occurrence of trees in those classes, the standard errors were very high and estimates are therefore to be treated with care. Another difference occurred in the smallest diameter class of trees (dbh 40-60 cm). Here the calculated abundance of stumps was twice as large as the numbers of podocarps encountered in the old-growth forest and the selective harvesting blocks. It is very likely that these stumps do not represent podocarps but were felled angiosperms such as *B. tawa*, *K. excelsa* and *E. dentatus*. Due to the limited scope of this study, no wood samples were collected from stumps to definitively identify species. But in the selective harvesting blocks, between 26 and 41 % of cruised angiosperms of the above

species were harvested in 1961 (Table 34) and it is likely that in the Māori blocks those species were also harvested in addition to the podocarps. The diameter distribution of podocarps between 40 and 200 cm dbh showed a bell-shaped curve with a maximum in the 100 cm class. Based on findings in Chapter 3, these trees seem to reflect a cohort of senescent emergent trees. With podocarps of diameters < 70 cm being scarce, this cohort will not be replaced by advancing regeneration in the foreseeable future (Beveridge & Herbert, 1978) under current conditions.

In the old-growth forest and in all blocks, emergent podocarps occurred either as single individuals or in small groups. This is reflected in the large standard error for the podocarp density in the Māori blocks. At some sites they were completely absent. A comparison of the pre-harvesting forest structure in the different forest blocks based on the harvesting inventory and on an aerial photograph from 1950 did not show significant differences between the blocks and podocarp frequencies, and abundances were therefore treated as comparable. No information is, however, available about pre-harvesting frequencies and abundances of smaller trees.

4.4.2. Canopy gaps

The gap size inventory showed that small gaps of 57-402 m² are the most common size in old-growth forest. They indicate a typical gap-phase regeneration cycle that was also observed in other podocarp-broadleaved forests in New Zealand (M. C. Smale & Kimberley, 1983, 1993; K. J. Whaley, 1996). In the selective harvesting trial, gaps of mainly 372-724 m² were created and did therefore not mimic natural disturbances in this forest type. This is in contrast to earlier subjective observations where selective harvesting at Pureora was thought to have mimicked natural disturbances in old-growth forest (M. C. Smale, Fitzgerald, & Bartlam, 2008). The gaps that were created during selective harvesting also differed in their structure from those in the old-growth forest, as the objective of the harvesting trial was to minimise damage to the forest structure by felling trees into already existing gaps (Beveridge & Herbert, 1978). High-grading of the Māori blocks on the other hand, where the majority of gaps ranged from 720-1249 m², did not try to minimise disturbance, as the idea was to later convert the blocks into an exotic tree plantation, the common practice at that

time (Fleet, 1986; M. C. Smale & Beveridge, 2007). Even though gaps with obvious soil disturbances such as skidder tracks and landings were excluded from this study, surface topsoil disturbance through hauling was extremely difficult to detect 56 years after harvesting and could therefore not be ruled out completely. The numbers of gaps in the different gap size classes in the Māori blocks increased with gap size and were highest in the largest gap size class of 1001-1250 m².

Gaps change in size and shape over the years through canopy expansion of edge trees, death or retreat of exposed canopies or senescent edge trees and ongoing gap formation events such as windthrow (Allen et al., 2014; Runkle, 1982). Therefore, gap size measurements 56 years after gap creation are difficult and prone to inaccuracy. Using geo-referenced aerial photographs that were taken in 1950, 1963, 1984, 2010 and 2012 helped to locate changes and exclude gaps that expanded considerably in size but slight changes are likely to be undetected in particular when gaps expanded between the beginning of harvesting in 1956 and the aerial photograph taken in 1963. But as this was still considered to be the gap formation process, it was neglected when taking gap measurements.

The sizes of gaps were hypothised to play an important role in tree species regeneration but the gap shape has also an important influence on growth conditions inside gaps (Fahey & Puettmann, 2008; Hu & J. Zhu, 2009; Hu, Yan, Wu, & J. Li, 2010; Schliemann & Bockheim, 2011; Seidel, Ammer, & Puettmann, 2015). But as gaps were created decades ago and historical gap shapes are extremely difficult to reconstruct reliably, the exact shapes of measured gaps and their effect on tree species regeneration was not investigated further.

4.4.3. Species frequencies

Significant relationships between presence of species and gap size were found for most species that occurred in more than 20 % of the gaps. No infrequently occurring species (19 out of 35) showed significant relationships. *Dacrydium cupressinum* and *P. ferruginea* were the only podocarps, where frequencies of occurrence were affected by gap size, while observations for the other podocarps were too scarce to be reliably modelled. Therefore, care should be taken when interpreting the results for scarce tree species. While

relationships for *B. tawa* and *E. dentatus* were significant, observations for *E. hookerianus*, *K. excelsa* and *N. cunninghamii* were scarce and relationships might still exist even though they were not visible. It is possible that other growth influencing factors override the effects of gap size (Kern, Reich, Montgomery, & Strong, 2012). The same problem occurred for all smaller tree species except the 7 most frequent ones and also for the tree fern *C. dealbata*. Excluding those species that were scarce, *N. lanceolata*, *M. ramiflorus* and the tree fern *C. smithii* were the only species that showed no significant relationship between species presence and gap size. *Beilschmiedia tawa* and *D. squarrosa* were the only species to show a significant negative correlation, while the significant relationships of all other species were positive. Lusk & Laughlin (2017), who sampled seedlings and saplings in natural treefall gaps of 20-30 m length, found that *B. tawa* and *K. excelsa* are typical understorey trees while *E. dentatus*, *C. serratus*, *M. ramiflorus* are more often found in treefall gaps. On the other hand, *Dacrydium cupressinum*, *E. dacrydioides*, *P. corymbosa* and *P. tenuifolium* were mainly found at clearing margins, exhibiting their competition success in particular light-environments.

Many tree species showed unimodal relationships between species presence and gap size. This means that after reaching their ecological optimum, their presence in gaps declined again. Other species did not reach an optimum yet or appeared in frequencies that were too low to detect optima. But the species response curves do not necessarily relate to increasing light levels alone. They could also be a result of correlating gradients such as soil properties (Fischer, Michler, & Ewald, 2014) or temperature (Olthoff et al., 2016) or a combination of several ecological factors (Austin, A. O. Nicholls, & Margules, 1990). Soil nutrients are extremely important factors for the successful establishment of tree species (Carswell, Whitehead, G. N. D. Rogers, & McSeveny, 2005; Coomes et al., 2005). In particular, soil nitrogen (N) is important for the successful establishment of *D. dacrydioides* and *P. taxifolia*, while numbers of seedlings of *P. ferruginea* and *D. cupressinum* were found to decline with increasing levels of soil phosphorus (P) (Carswell et al., 2007). The creation of harvesting gaps increases mineralisation rates of N as well as mineral N concentrations as a result of increasing soil temperature and water content (Coulombe, Sirois, & Paré, 2017) and levels

are likely to have increased with large gap formation after high-grading (Hazlett, Gordon, Voroney, & Sibley, 2007).

The four most frequently occurring large tree species were *B. tawa*, *P. ferruginea*, *E. dentatus* and *D. cupressinum*. Here, *B. tawa* was the species with the overall largest frequency. After reaching its maximum at a gap size of 616 m², its presence began to decline again while values for *P. ferruginea* and *D. cupressinum* were still increasing. But it was not before a gap size of 1175 m², shortly after *D. cupressinum* reaches its maximum at 1042 m², that *B. tawa* had the same probability of occurrence as *P. ferruginea* and *D. cupressinum*. This means that even though *B. tawa* was the most frequently occurring species in all small and medium gaps, it was losing its dominance in larger gaps until it had the same probability of occurrence in the largest gaps as *P. ferruginea* and *D. cupressinum*. The other podocarps were too scarce to be reliably modelled even though *P. taxifolia* and *P. totara* showed a trend towards an increase in presence with gap size. *Nestegis lanceolata* showed a maximum probability at 596 m², suggesting that it prefers medium sized gaps to larger ones. The question remains, why the presence of *B. tawa* declined significantly when gaps were getting larger as this is not the case for all smaller tree species, which steadily increased in their probability of occurrence up to the largest gaps without approaching an optimum or an asymptote in the largest gap size. *Beilschmiedia tawa* is known for its frost intolerance, and it is possible that low temperatures in large gaps affected its regeneration success (Kelly, 1987) as temperatures in large gaps rather resemble those in open land than under a closed canopy or in small gaps, and frosts can be quiet severe (Davies-Colley, Payne, & van Elswijk, 2000; Lowe & C. M. King, 2015).

Melicytus ramiflorus seems to have no preferences regarding an optimal gap size as it occurred in all gap sizes similar frequently. Once again, modelling results for species that are scarce are prone to error, even though the trend of increasing presence with increasing gap size was consistent with the relationship of more frequent species. *Dicksonia squarrosa* was the most frequently occurring tree fern species in all gap sizes, even though its presence declined significantly with gap size. On the other hand, the presence of *D. fibrosa* increased continuously with gap size and is about equal to *D. squarrosa* in the largest gaps.

Overall, the numbers of species increased with increasing gap size, a phenomenon that is also known from other forest types (Denslow, 1995). Light-demanding tree species were the main contributors to the increase in species diversity, an observation that was also made in other studies that investigated the effect of gap size on tree species diversity in complex forests (Schnitzer & Carson, 2001).

The diameter distribution of the different species shows that 56 years after high-grading of the Māori blocks and 52 years after selective harvesting in the FRI blocks, podocarps of all diameter classes up to 40 cm dbh are found in the different gap sizes, the majority of trees having diameters around 20 cm in *D. cupressinum* and around 30 cm in *P. ferruginea*. It is interesting to note that with increasing gap size, scarce podocarp species such as *D. dacrydioides* and *P. taxifolia* move from diameter class 1 in the smallest gaps to diameter classes 3 and 4 in the larger gaps. This observation that increasing gap sizes enhance diameter growth of light-demanding species has been also made in other forests types where shade-tolerant and light-demanding tree species coexist (Wiser, G. Baker, & Benecke, 2007). But numbers of observations were generally low due to the scarcity of trees of those species and results need to be interpreted with caution. This effect is not visible for any of the large angiosperm tree species, where diameter distributions were not affected by gap size, in particular for *B. tawa* and *E. dentatus*. The small tree species *C. serratus*, *C. australis*, *P. arboreus* and *P. crassifolius*, however, showed a trend similar to *D. dacrydioides* and *P. taxifolia*, where increasing gap size correlates with increasing diameters of trees.

The effect of gap size on the different social classes of trees for *D. cupressinum*, *P. ferruginea*, *B. tawa* and *P. crassifolius* is in line with the overall trend for those species, whereas in case of *E. dentatus*, *C. serratus*, *C. australis*, *P. arboreus* and *W. racemosa* only the higher social classes show significant positive correlations between species presence and gaps size. This could be again due to the fact that trees of lower social class 5 of those species were too scarce to be reliably modelled.

Modelling the effect of gap size on the presence of trees for different social classes of trees separately allowed not only a comparison of the response of trees of different social classes

but also a clearer view of the relationships between species in the same social class. The most dominant trees 56 and 52 years respectively after harvesting are codominant class 3 trees. They represent a cohort that will, without further widespread disturbance, form the future main canopy of the forest. Therefore, the species distribution within this class is a good indicator for the future forest canopy structure. Figure 71 shows that even though *B. tawa* is the most frequently occurring species in small and medium-sized gaps, it is overtaken by *P. ferruginea* at a gap size of around 825 m² and by *D. cupressinum* at around 975 m². This means that as the sizes of gaps in the forest change the probable species composition of the future main canopy also changes significantly. Observations of the other podocarp species in social class 3 indicate that there is an increase in presence with increasing gap size, with *D. dacrydioides*, *P. totara* and *P. taxifolia* found only in the largest gaps. But with those species occurring only infrequently, no reliable predictions can be made regarding their response to changes in gap size. Among the subdominant trees of social class 4, *B. tawa* remains the most frequently occurring tree species in gaps of all sizes. In gaps of 1000-1150 m², *E. dentatus*, *P. ferruginea* and *D. cupressinum* occur similarly frequently in gaps. Trees of this social class were generally of the same age as trees of social class 3 but had slower radial growth. Even though these trees are already outcompeted by class 3 trees, they still reflect a social class that can potentially recruit into social class 3 in case of unexpected canopy disturbances. The other podocarp species are scarce in social class 4, with the exception of *P. taxifolia*. This supports the light-demanding character of *D. dacrydioides* and *P. totara*. Dominated trees of social class 5 occur considerably less frequently than trees of the other social classes. These trees are again generally of the same age as other trees of higher social classes in those gaps. They are currently not able to advance into higher social classes and are likely to linger in the understorey until they either die or the newly formed canopy opens up again and improves the growth conditions for them. But the reasonably large frequencies of occurrence of *B. tawa*, *P. ferruginea* and *D. cupressinum* in this class underline their ability to withstand substantial shading for some time. The smaller tree species show an increase of occurrence with increasing gap size throughout social classes 3 and 4. This exhibits their light-demanding character, in particular in the case of *C. serratus*, *P. arboreus*, *P. crassifolius*, *C. australis* and *W. racemosa*. While they appear frequently in the largest gaps, they are scarce in social class 5. They were found

to be a typical feature of large gaps and will most likely disappear when a new canopy of taller trees closes above them as they are physiologically incapable of reaching the main canopy. However, previous studies did not find specific correlations between *W. racemosa* occurrence and canopy gap size (Lusk & Ogden, 1992; G. H. Stewart & Veblen, 1982). Instead, they found continuous regeneration of this species even in closed forest. But those studies were investigating different types of forest and it is likely that light environments in those forests differ from podocarp-broadleaved forest at Pureora.

4.4.4. Species abundances

While the presence of species in gaps is an important indicator for the distribution of species within the forest, the abundances of trees of the different species will determine their dominance in the future forest. *Beilschmiedia tawa* was the most abundant tree species, but after reaching it maximum abundance at 463 m², it began to decline until *D. cupressinum* surpassed it at a gap size of 710 m², as did *P. ferruginea* at a gap size of 820 m². This was just before *P. ferruginea* reached its maximum abundance at 852 m². It shows clearly that *D. cupressinum* and *P. ferruginea* benefit from large gaps for successful advanced growth. It also shows that gaps of 850-1100 m² promote a forest canopy structure that is dominated by *D. cupressinum* and *P. ferruginea*. With gaps getting larger, the abundances of those species declined significantly. Those gaps were mainly found in the high-graded Māori blocks and it can be assumed that the creation of those large gaps was accompanied by large-scale destruction of seedlings and saplings that were present at that time. An indication is the strong negative correlation between age and gap size. In particular in the largest gaps, existing trees got established mainly after harvesting, while trees in smaller gaps were already present as seedlings and saplings before harvesting.

Elaeocarpus dentatus of social class 3 and 4 occurred frequently in a wide range of medium to large gaps but it was never abundant. Its maximum abundance in medium-sized gaps at 713 m², however, coincides with its maximum frequency at 774 m² of social class 3 trees and 714 m² of trees of social class 4. This also means that *E. dentatus* had its maximum abundance when *B. tawa* and *D. cupressinum* occurred in equal abundances. While most

other large tree species were rare, *D. dacrydioides* showed a strong increase in abundance with increasing gap size. This means that even though this species did only occur infrequently in gaps, it was likely to be abundant when it did. Therefore, factors other than gap size must have a large effect on the distribution of *D. dacrydioides* in the forest. This seems to be similar for *P. totara*, which was absent in small gaps but occurred infrequently in large gaps and when it did, it was likely to be abundant.

The small tree species were not particularly abundant in gaps at all, with the exception of *P. arboreus*, *P. crassifolius* and *W. racemosa*. Numbers of trees only increased slightly with gap size. Among the tree ferns, *D. squarrosa* was the only species that can be considered abundant and showed a proportional increase of abundance with gap size. This in fact means that its relative abundance did not actually increase but was stable up to 1104 m² after which numbers dropped.

The abundances of codominant social class 3 trees were much lower than the overall abundances, indicating a mixture of trees of different social classes within gaps. At gap sizes of 500-550 m², codominant trees of *B. tawa* became less abundant than *D. cupressinum* and *P. ferruginea* and at 600 m² even less abundant than *E. dentatus*. But the almost proportional increase in the absolute abundances of *D. cupressinum* and *P. ferruginea* with increasing gap size accompanied by a decrease in the relative abundances of all other tree species increases the dominance of those two species. Even trees of lower social classes of those species had, with an increasing gap size, an increasing chance to change into higher social classes and become dominant in the future canopy of the forest.

When the increase of the absolute abundance is less than proportional to an increase of gap size, the relative abundance (numbers of trees per hectare) actually decreases. Taking an abundance of 5 trees of *D. cupressinum* in a gap of 200 m² as a reference, a gap of 400 m² must carry more than 10 trees of that species to actually show an increase in relative abundance. The only species doing so were *D. cupressinum*, *P. ferruginea* and the tree fern *D. squarrosa*. This means that the increase of absolute abundances of all other species actually represents a decrease in their relative abundance. This becomes visible when

calculating the numbers of trees per hectare, which decrease with increasing gap size. Besides low light levels in small gaps, the competition with tree ferns was found earlier to be an important factor that prevents successful podocarp regeneration in podocarp-broadleaved forest (Beveridge, 1973; Coomes et al., 2005) and the high abundance of *D. squarrosa* is likely to prohibit prolific regeneration of trees in gaps. Another factor that might influence the frequency and abundance of tree species is soil drainage (Urlich et al., 2005). In particular, *P. taxifolia* is known to prefer well-drained soils for successful establishment, while *D. dacrydioides* can persist on wetter sites (G. H. Stewart, 2002).

4.4.5. Age structure

Trees that were occurring in gaps do not share the same age class but established at different times over the past 130 years. But boosts of successful recruitment that occurred in 1935/40 and after 1955/60 are also visible. The first date coincides with the devastating cyclone that hit the North Island in February 1936 (Chapter 3), while the second date coincides with high-grading in 1956/58. Light-demanding podocarps such as *P. trichomanoides*, *P. taxifolia*, *D. dacrydioides* and *P. totara* seem to need those large disturbances to establish successfully. Similar observations were made by Lusk & Ogden (1992), who found that the spread of age classes in a forest reflects differences in light-regimes, where shade-tolerant species show a continual presence in all age classes, while light-demanding species only establish after substantial disturbances, forming cohorts of similar aged trees. The resulting forest contains accordingly so called birth-flow and birth-pulse populations (Caswell, 2001).

Trees that are found in gaps today and that were already present in 1936 were at the time of the cyclone only seedlings or saplings with suppressed growth. Seedlings of *P. ferruginea* and *D. cupressinum* are able to survive under unfavourable light conditions for many years and wait for growth conditions to improve (Allen et al., 2014; Lusk et al., 2009). But due to the trade-off between shade tolerance and growth, they are unable to advance in small canopy gaps (Lusk et al., 2015). For instance 30 % of the trees of *D. cupressinum* that are found in gaps today were already present as seedlings at the time of the cyclone in 1936. But

according to the number of individuals found in small gaps, it is doubtful that these seedlings would have been able to become the subdominant trees they are today if light conditions had not improved considerably and led to a substantial growth release.

High-grading in 1956/58 led to a continuous increase in successful recruitment of all species by creating a disturbance large enough to enhance growth conditions for a long time. Exposure and wind damage can be expected to have continued to change the forest structure long after felling. Light-demanding podocarps such as *P. totara, D. dacrydioides*, *P. trichomanoides* and *P. taxifolia* were very scarce in the old-growth forest and seem to require substantial disturbance for successful recruitment.

All trees of those species were found to have established at the time of the cyclone or at the time of high-grading. There is no record, however, if that event coincided with a seeding mast. In none of the sampling plots, *B. tawa* regeneration was found that established in the wake of the cyclone and only few were found to have established after high-grading, leading to the conclusion that this species does not favour large-scale disturbances. One explanation for these extremely low numbers in large gaps in particular could be its frost intolerance, particularly of newly exposed trees (Knowles & Beveridge, 1982; Mackenzie & Gadgil, 1973; M. C. Smale & Kimberley, 1983).

The negative relationship between tree age and gap size was strongest for *D. cupressinum*, followed by *E. dentatus*. For P. *ferruginea* and *B. tawa* this relationship was not as significant but still evident. The majority of trees of *D. cupressinum*, P. ferruginea, *B. tawa* and *E. dentatus* in smaller gaps established before the devastating cyclone in 1936 and were at that time small seedlings or saplings. In medium-sized gaps, harvesting will have destroyed many of the larger and older established trees as they will have been prone to felling damage, while smaller trees and seedlings survived unharmed. It case of *B. tawa* is also possible that some may have coppiced from intact root systems that survived stem breakage (M. C. Smale, 1982). In cases where high-grading was most destructive, forming the largest gaps, small tree species and shrubs as well as seedlings of *D. cupressinum* established after harvesting ceased.

The time of gap creation is difficult to estimate as the size of gaps can change over time. While small gaps can be closed very quickly by residual trees, large gaps can extend in size by repeated disturbances. Once the canopy of the forest is opened up, trees bordering a gap can die due to the sudden exposure or the pre-existence of stem or butt rots. In addition, subsequent windthrow can extend gaps over years significantly (Runkle, 1982; Schliemann & Bockheim, 2011). This may result in trees of different age classes filling the same gap, which could potentially obscure modelling results as older trees may have established in gaps that were previously smaller. Even though aerial photographs were used to compare gaps sizes over time, small changes cannot be ruled out and are likely to have occurred.

4.4.6. Diameter growth

The mean annual increment of all tree species was larger than that reported in studies of old-growth forest (Hurst et al., 2007; M. C. Smale et al., 2014). *Dacrydium cupressinum*, *P. ferruginea*, *B. tawa* and *E. dentatus* showed positive correlations between annual mean diameter increment and gap size, apart from *B. tawa* and *E. dentatus* in social class 4. In particular *D. cupressinum* was able to increase its annual diameter increment by over 100 %. Increasing gap sizes influenced its diameter growth significantly more than the growth of the other species. This supports the theory that *D. cupressinum* needs a substantial opening in the canopy for advance growth and to be able to compete with the other three species. Growth rates for *B. tawa* and *P. ferruginea* differed not much in social class 3, even though *B. tawa* was surpassed by *P. ferruginea* and *D. cupressinum* at a gap size of around 450 m². Trees of social class 3 represent the future main canopy. The ability of *D. cupressinum* to respond to increasing gap sizes with a significant increase in growth that surpasses *B. tawa* and *P. ferruginea* can change the structure of the future forest considerably. While small gaps promote a forest that is dominated by shade-tolerant species, large gaps promote the growth of *D. cupressinum* and to a degree of *P. ferruginea* and with that their abundance as dominant trees in the forest. Comparing the mean annual diameter increments of *D. dacrydioides*, *P. trichomanoides*, *P. totara* and *P. taxifolia* indicates that these species also have the potential to outgrow *B. tawa* (Bergin & Kimberley, 2003; M. C. Smale et al., 2014). But these conclusions are based on diameter increment alone, while height increment is an

even more important predictor for the future forest structure. However, past height increments of trees at the study site are difficult to sample non-destructively.

4.4.7. Release and suppression

Abrupt variations in radial increment were visible in growth rings of all species of interest. Those changes could be confined to individual trees, small groups of neighbouring trees, or affect the whole forest. Changes of radial growth that affected the largest numbers of trees coincide with major climatic disturbance events such as the devastating cyclone in 1936 (Chapter 3) or cyclone Bola in 1988. This is in line with observations of other authors who investigated the effects of severe windthrow events (Martin & Ogden, 2006). But large-scale growth releases were also found to coincide with destructive harvesting in 1956/58. The species that benefitted the most from high-grading were *P. ferruginea* and *E. dentatus*.

While those growth releases in the wake of large-scale disturbances were found to promote growth of all species, these events seemed to be particularly important for tree species that are scarce in the forest. One particular species is *D. cupressinum* which, apart from emergent individuals, is scarce in the old-growth forest in diameters above 2.5 cm even though it is reasonably abundant in the seedling stage. The cyclone of 1936 enhanced growth of a cohort of those seedlings on a large scale and a subsequent growth release after high-grading in 1956/58 seemed to have been essential for their survival and today's dominance. This second release did not occur in the old-growth forest and trees of *D. cupressinum* remain scarce, even though the cyclone of 1936 resulted in an initial growth release there as well (Chapter 3). A similar observation was made for the other scarce podocarp species *D. dacrydioides*, *P. taxifolia*, *P. totara* and *P. trichomanoides*. All trees of those species in gaps established in the wake of the cyclone of 1936 and after high-grading in 1956/58. In particular, the large-scale disturbance of high-grading favoured successful recruitment of *P. totara*. These podocarp species are still extremely scarce in the old-growth forest but are now found infrequently in the high-graded Māori blocks. The overall suppression of growth from the late 1990s onward seems to indicate that neighbourhood competition is now affecting previously released trees. But as no spatial analysis was carried out in this context, this hypothesis cannot be proven.

4.5. Conclusion

Does selective harvesting mimic the natural disturbance regime in podocarp-broadleaved forest?

A comparison of the distribution of different-sized gaps in old-growth forest, selectively logged forest and high-graded forest showed that 70 % of the natural gaps in podocarp-broadleaved forest at the study site were smaller than 400 m², while the majority of selective harvesting gaps were between 372 and 724 m² and 70 % of the gaps in the high-graded forest between 720 and over 1249 m². This means that neither silvicultural regime mimicked the general small-scale disturbance pattern in old-growth forest. But infrequent large-scale disturbance events such as the cyclones in 1936 and 1988 were found to have effects similar to large gaps created by anthropogenic disturbance.

What are the long-term effects of harvesting gap size on species composition in podocarp-broadleaved forest?

The size of harvesting gaps was found to have a significant long-term effect on the species composition in podocarp-broadleaved forest 56 years and 52 years respectively after harvesting. Among the tree fern species, *D. fibrosa* increased continuously in frequency with increasing gaps size, while *D. squarrosa* decreased in frequency and abundance in large gaps. Small harvesting gaps (<400m²) did not change the forest structure significantly and species composition is similar to natural gaps in old-growth forest. The only tree species found in those small gaps are shade-tolerant tree species such as *B. tawa*, *P. ferruginea* and *E. dentatus*. Medium-sized gaps (400-800 m²), occurring primarily in selective logging, increased the frequencies and abundances of those shade-tolerant species that reached a maximum in gaps of 600-800 m². In those gaps, shade-resistant *D. cupressinum* and light-demanding species such as *P. crassifolius*, *P. arboreus*, *W. racemosa* and *C. serratus* also became more abundant but were still dominated by the shade-tolerant species. In particular, suppressed seedlings and saplings of *D. cupressinum* that established before harvesting were able to benefit from the changed light environment and advance into the subcanopy. Even though these seedlings and saplings are shade-resistant when young, they need substantial openings in the canopy for advanced growth. Where gaps are already

closing, these trees now show suppressed growth. The light-demanding angiosperms that are physically not able to grow into the main canopy are likely to disappear once the gaps are closed again by tall large-crowned trees. Larger gaps (800-1000 m²), on the other hand, caused a substantial change in forest composition, with shade-tolerant species declining significantly and light-demanding species become more dominant. Early successional angiosperms such as *C. australis*, *G. littoralis*, *P. tenuifolium* and *K. ericoides* s.l. become abundant and light-demanding podocarps *D. dacrydioides*, *P. totara* and *P. taxifolia* begin to appear. However, C. australis, P. tenuifolium and K. ericoides are likely to disappear either as a consequence of age, or being overtaken by other taller growing species. *Dacrydium cupressinum* and *P. ferruginea* have their maximum frequency and abundance in these gaps. Due to the lack of competition from other large tree species, the podocarps are likely to retain their dominance in those gaps even after they are closed. Later appearing shade-tolerant species will not be able to compete with advanced podocarps once they have passed the main canopy height. In the long term, this disturbance level is likely to promote a forest type where podocarps dominate above a closed canopy of shade-tolerant angiosperms. Harvesting gaps >1000 m² throw succession back to an early stage and are still in the open gap phase. Even 56 years after harvesting, these gaps lack significant regeneration of trees. This becomes evident when the absolute abundances of trees (trees per gaps) are converted into relative values (trees per hectare), where the densities of trees become lower in larger gaps. Destructive harvesting seems to have destroyed the majority of already established seedlings, saplings and pole trees. The light-demanding early successional tree and shrub species in those gaps are still competing with invasive introduced blackberry (*Rubus fruticosus*) as well as tall grasses (*Austroderia fulvida*) and sedges (*Carex* spp.), and it can be expected that it will take at least another 50 years until those large gaps are covered by forest again.

What is the impact of different scale canopy disturbances on the diameter increment rates of trees in gaps?

Diameter increment modelling showed that mean diameter increments of *B. tawa*, *E. dentatus*, *D. cupressinum* and *P. ferruginea* increased with increasing gap size. This increase was most evident in trees of social class 3, the highest social class found in gaps. *Elaeocarpus*

dentatus was overall the fastest growing species in all gap sizes. *Beilschmiedia tawa* and *P. ferruginea* were growing equally fast in small gaps, where *D. cupressinum* was the slowest growing species. Even though diameter increment of all species increased with gap size, *D. cupressinum* showed the strongest relationship and surpassed *B. tawa* and *P. ferruginea* in diameter growth at a gap size of 450 m². In the largest gaps, it was growing almost as fast as *E. dentatus*, proving that while *D. cupressinum* is able to survive in low light conditions, it shows its best growth performance in large gaps, where it is able to outcompete the shade-tolerant species.

What canopy disturbance regime do podocarps require for successful recruitment and subsequent growth?

The different podocarp species show different responses to canopy openings, depending on their light requirements. *Prumnopitys ferruginea* was able to benefit even from small canopy openings < 200 m², while *D. cupressinum* needed gaps of at least 400 m² for improved growth. The optimal gap size, where both species reached their maximum dominance, was around 850-950 m². These were also the gap sizes where *D. dacrydioides* and *P. totara* were found most often, even though they remained generally scarce. *Prumnopitys taxifolia* occurred mainly in gaps >1000 m². This means that while small-scale disturbances are maintaining the general forest structure with an only very small podocarp component, larger disturbances enhance growth conditions for podocarps significantly and enable their successful advance into higher classes.

The age study revealed that gaps in the building phase are dominated by trees that established between 1900 and 1935. The catastrophic cyclone of 1936 initiated a growth release that enabled suppressed seedlings and saplings to advance into larger size classes. With harvesting initiating another growth release 20 years later, those trees finally secured their dominance in gaps. This was particularly the case for *B. tawa*, *E. dentatus*, *P. ferruginea* and *D. cupressinum*. Each of those disturbance events also initiated successful regeneration of further trees of those species. A similar release effect was visible after the cyclone Bola in 1988.

Gap formation is not always a single event in time, but can be a continuing process that can take decades. While some gaps close shortly after creation, others increase in size through repeated disturbances. The gaps that were investigated in this study were examples of the ongoing changes in growth conditions in gaps caused by repeated disturbances. While small-scale disturbances are common features of old-growth podocarp-broadleaved forest at the study site, large-scale disturbances were the main creators of significant changes in the future forest structure. The age distribution of trees in gaps shows that periodic significant gap formation events such as destructive cyclones and high-grading enhance the regeneration success of *P. ferruginea* and *D. cupressinum* significantly and are crucial for successful recruitment of *P. trichomanoides*, *D. dacrydioides*, *P. totara* and *P. taxifolia*.

Chapter 5

Sustainable management of podocarp-broadleaved forest – are we asking for the moon?

5.1. Introduction

This doctoral research compared the structure and dynamics of old-growth podocarp-broadleaved forest with podocarp-broadleaved forests 56 years after high-grading and 52 years after selective harvesting. In particular, the effects of different scales of canopy disturbance on the forest structure were examined. Furthermore, it elaborated requirements of the different tree species involved for regeneration and subsequent growth, and highlighted several challenges for indigenous forestry managing this forest type.

This final chapter summarises the findings of the three previous chapters. Results will be used to assess whether the silvicultural prescriptions specified in the amended Forests Act are sufficient to meet the objectives of the Act in the case of podocarp-broadleaved forest, as it occurs in the research area in Pureora Forest.

5.1.1. The nature of growth

Non-destructive tree ring analysis of 5.0 mm bark-to-pith increment cores was the standard method for the age as well as increment studies. The case of *B. tawa* proved, however, that even when tree rings are distinct, such studies are charged with uncertainties when underlying assumptions of tree core analysis are violated. These assumptions are that rings are formed annually and that the width between two rings represents the growth of a tree in a particular year. But false, missing and incomplete rings as well as irregular, eccentric and lobate growth pose considerable uncertainties in age, diameter and increment estimates. Cross-dating can reduce the uncertainties when mean sensitivities are low and ring widths are consistent.

Twin cores of a tree taken at a horizontal angle of 90° to each other can be used to investigate uncertainties in ring pattern characteristics. The closer twin cores match, the less likely is it that the underlying assumptions are violated. But they do not necessarily enable the detection of false and missing rings, particularly for suppressed trees. Where annual rings are missing, age estimates as well as increment calculations of those trees may contain considerable errors. The increment calculations in this study therefore used periodic mean

annual increments instead of actual annual increment. The only resolution for this problem would have been complete cross-sectional stump-height discs, but this was not an option in this study.

Therefore, age estimates of individual trees have to be treated with some caution unless correlations can be made with known dates of events such as the cyclone of 1936 or harvesting operations that changed growth conditions in the forest can be used for changepoint analysis that enables dating of release events and therefore for accounting for false and missing rings. Individual errors of overestimation and underestimation of calculated increment of *B. tawa* were found to balance each other out on a stand basis, which made stand-level predictions as reliable as possible.

5.1.2. Podocarp-broadleaved forest in the Central North Island

The present structure of old-growth podocarp-broadleaved forest on the Volcanic Plateau at Pureora exhibits an emergent tier of senescent podocarps of *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, *Dacrycarpus dacrydioides* and *Podocarpus totara* above a dense canopy of mature shade-tolerant *Beilschmiedia tawa* and scattered *Elaeocarpus dentatus*. Below this main canopy, the subcanopy is dominated by medium-sized *B. tawa*, with scattered *P. ferruginea* and *E. dentatus* also being present. Tree ferns such as *Dicksonia squarrosa* and *Cyathea smithii* are frequent in the shrub tier. Seedlings up 1.5 m height of *B. tawa*, *P. ferruginea* and *D. dacrydioides* are widespread throughout the forest and abundant. *Dacrydium cupressinum* also occurs in reasonable numbers, while *P. taxifolia* is rather rare and *P. totara* is absent. But in sapling classes, only *B. tawa* occurs in large numbers, along with reasonably abundant *P. ferruginea*. *Dacrydium cupressinum* and *P. taxifolia* are rare.

This forest structure is indicative of the light-requirements and competitive advantages of the different species for establishment and subsequent growth, although the individual species requirements may change during different life-stages. In particular, the dominance of *B. tawa* in all diameter and height classes highlights its tolerance to the low light conditions in this forest beneath the main canopy. *Prumnopitys ferruginea* is the only

podocarp species that can grow, even if only very slowly, under those conditions. Even though seedlings of the podocarp species *D. dacrydioides*, *D. cupressinum* and *P. taxifolia* can survive in low light conditions for some time, they require higher light levels for sustained growth and survival.

The patchy mosaic of the forest is shaped by small-scale natural disturbances such as single tree death and occasional localized windthrow, reflecting a growth cycle that involves gap, building and mature phases. The gap phase at Pureora does not seem to create disturbances conducive to successful podocarp regeneration, and is a possible cause for the 'regeneration gap' of podocarps. Under these conditions, the fast declining emergent podocarps will not be replaced and the podocarp-broadleaved forest will slowly succeed into a *B. tawa* dominated forest with widely scattered podocarps, in particular *P. ferruginea*.

Infrequent catastrophic events, however, can create canopy disturbances that are large enough for growth releases of light-demanding tree species. This was evident in 1936, when one of the most devastating cyclones of the 20th century hit the North Island of New Zealand. A significant growth release in the years that followed was identified in *D. cupressinum*, *P. ferruginea* and *D. dacrydioides*, and also *B. tawa*. Most medium-sized podocarps that are today part of the subcanopy of the forest were seedlings or small saplings at that time. However, since the mid 1990s, the number of podocarps with suppressed growth has increased. The results of this study indicate that another catastrophic event would be necessary for their progression into the main canopy. Once they emerged from the main canopy, they would eventually replace the declining cohort of emergent podocarps.

5.1.3. The positive impact of large disturbance

The majority of naturally occurring gaps in the old-growth forest were smaller than 400 m². In a 1961 selective harvesting trial at Pureora, the majority of harvesting gaps ranged from 374 to 724 m² and were therefore in general much larger than naturally occurring gaps. High-grading of podocarp-broadleaved forest created even larger gaps between 720 and over 1249 m².

In particular, *B. tawa*, *E. dentatus*, *P. ferruginea* and *D. cupressinum* benefitted the most from larger canopy openings. Codominant *Beilschmiedia tawa* had the highest frequency of occurrence of all species in all gaps below 825 m² with an optimum gap size of 688 m². In gaps larger than 825 m², codominant trees of *P. ferruginea* became more frequent than *B. tawa* and at 975 m² *B. tawa* was surpassed by *D. cupressinum*. In gaps larger than 1050 m², codominant *D. cupressinum* was the species that occurred most often. This means that even though selective harvesting gaps increased the occurrence of podocarps slightly, it favoured *B. tawa* even more, while larger high-grading gaps favoured regeneration and subsequent growth of the podocarps *P. ferruginea* and *D. cupressinum*.

Abundances of the different tree species had a similar relationship to gap size as frequencies. *Beilschmiedia tawa* was the most abundant tree species in all gaps up to 710 m², with its maximum abundance at 463 m². In gaps larger than 710 m², *D. cupressinum* was the most abundant tree species with its maximum at 963 m². *Prumnopitys ferruginea* surpassed *B. tawa* in abundance at a gap size of 820 m².

Small gaps, whether created naturally or by harvesting, will favour regeneration of *B. tawa* and without larger disturbances will maintain its dominance in the forest. Even though podocarp regeneration is likely to increase in dominance in some medium-sized gaps, it is not until gap sizes of 700-800 m² that *D. cupressinum* and *P. ferruginea* are as abundant as *B. tawa*. All other podocarp species are scarce in small and medium-sized gaps, but show an increase in frequency and abundance in large gaps.

The advantage of large disturbances for successful podocarp regeneration is also highlighted by the observation that the cyclone of 1936 and high-grading were followed by a massive increase of successful *P. ferruginea*, *D. cupressinum* and also *E. dentatus* regeneration. But while this effect lasted only for 5 years in the case of the cyclone, it lasted for almost two decades in the case of high-grading. This was particularly visible in *D. cupressinum*, where the increase in regeneration continued even for 20 years. Those large disturbances also allowed for *P. totara*, *D. dacrydioides* and *P. taxifolia* regeneration. These are podocarp species that occur frequently as emergents in old-growth forest but are extremely rare in all

smaller diameter classes. While *B. tawa* regeneration was also able to benefit immediately from those large disturbances, this effect was only immediate and did not last for long.

Not only regeneration increased after the catastrophic disturbances. Seedlings and saplings of *D. cupressinum* and *P. ferruginea* which established up to 20 years before the cyclone of 1936 and were suffering under the low light conditions in old-growth forest showed a strong growth release after the cyclone. Such a growth release was also visible after high-grading, where it led to a second release of the seedlings and sapling of 1936 as well as to a first release of those podocarps as well as *D. dacrydioides* and *P. trichomanoides* that established in the wake of the 1936 cyclone.

Dacrydium cupressinum and *P. ferruginea* have the potential to outcompete the overwhelmingly dominant species *B. tawa* in frequency, abundance, regeneration and subsequent growth, but only in gaps larger than 700 m² such as those that were formed after catastrophic disturbances.

5.2. The impact of selective harvesting

The podocarp-broadleaved forest on the Volcanic Plateau is currently in natural transition towards a broadleaved forest with an insignificant occurrence of podocarps. The only exception here might be *P. ferruginea*, which is the most shade-tolerant of the podocarp species. The emergent tier of senescent podocarps is disappearing relatively fast and, without larger disturbances, will not be replaced. The forest will continue to be dominated by *B. tawa*, with other angiosperms such as *E. dentatus* occurring infrequently. With the supply of podocarp seeds disappearing, regeneration of those species will become scarce and they might disappear from the forest in the long term unless large disturbances change growth conditions considerably. Good examples are *P. totara*, *P. taxifolia* and *D. dacrydioides*.

Harvesting in this forest type means typically the extraction of merchantable emergent podocarps with a minor percentage of *B. tawa* and *E. dentatus*. The aim of selective harvesting of single trees or small groups is to minimize disturbances in the canopy and to

maintain the forest structure. The 1961 selective harvesting trial showed that the main forest canopy did not collapse after harvesting. Basal areas of unharvested species seem to be similar to those in old-growth forest. The forest has the same number of tiers that are found in old-growth forest and the overall structure seems to be maintained (M. C. Smale & Beveridge, 2007; M. C. Smale et al., 1998). The selective harvesting trial demonstrated that it is possible to harvest 30 % of the volume of emergent podocarps without destroying the forest structure. It also showed that small harvesting gaps will close over time and that mortality rates of residual trees are similar to the old-growth forest (M. C. Smale, Fitzgerald, Arnold, et al., 2008).

But selectively harvested forest and old-growth forest differ significantly in many other respects (Gillman, 2008; Norton, 1996; D. A. Wardle et al., 2008). The first apparent difference is the loss of senescent trees. There is strong evidence that selective logging of senescent emergent podocarps has a negative impact on native bird life, in particular *Nestor meridionalis septentrionalis* (North Island kaka), *Callaeas wilsoni* (North Island kokako), *Prosthemadera novaeseelandiae* (tui) and *Hemiphaga novaeseelandiae* (kereru) even when small numbers of trees are harvested (J. C. Halkett, 1985; O'Donnell & Dilks, 1987; Warburton, Kingsford, Lewitt, & Spurr, 1992). These bird species feed on invertebrate larvae that colonize deadwood, as well as seasonal podocarp fruits. In addition, many vertebrate species use voids in senescent trees as habitats for nesting and roosting (Blakely & Didham, 2008; Sedgeley & O'Donnell, 1999). Vines and epiphytes rely on those trees as important habitats (K. C. Burns & Dawson, 2005) and standing dead and windthrown trees provide habitat for numerous invertebrate and fungal species (Beets et al., 2008; Blakely & Didham, 2008; Hood, 2012; Hood, Sandberg, & Kimberley, 1989). The function of these trees in the forest ecosystem as food source and habitat for bird, insect and plant species is not likely to be replaced by another generation of podocarps in the foreseeable future, which means that selective harvesting is likely to accelerate their decline.

Gaps 52 years after selective harvesting are closed mainly by angiosperms, predominantly *B. tawa,* or by tree ferns such as *D. squarrosa*. The small gaps that are created by selective harvesting do not favour regeneration of light-demanding species or species that need

increased light levels for subsequent growth (Putz, Sist, Fredericksen, & Dykstra, 2008). No significant numbers of trees of those species were found in advanced life-stages at the study site. The selective harvesting trial failed to prove that podocarps can successfully colonize small harvesting gaps. Even if selective harvesting does not destroy the forest, it accelerates succession from mixed podocarp-broadleaved forest to broadleaved forest with only insignificant numbers of podocarps (M. C. Smale et al., 1998). Similar observations were made in the eastern North Island's mixed podocarp-broadleaved forest of Te Urewera, where selective harvesting seems to change the forest structure from podocarp-broadleaved forest to a forest dominated by broadleaved tree species in the long term (Carswell et al., 2007).

5.3. Selective harvesting and the Forests Amendment Act 1993

Sustainable forest management is defined in the Forests Amendment Act 1993 as:

"... the management of an area of indigenous forest land in a way that maintains the ability of the forest growing on that land to continue to provide a full range of products and amenities in perpetuity while retaining the forest's values"

The terminology used here offers substantial room for interpretation. However, it is clear that the 'full range of products and amenities' is not provided 'in perpetuity'. When the numbers of emergent podocarps (dead or alive) in mixed uneven-aged podocarp-broadleaved forest are reduced, the habitats they provide for other species (birds, insects and plants) are also reduced, as no replacement of those senescent trees is in sight. In addition, the negative aboveground and belowground effects of selective harvesting on soil C sequestration, soil C:P and N:P as well as on soil microflora are generally neglected (D. A. Wardle et al., 2008). There is also well-founded concern that the current provisions of the Forests Amendment Act are inadequate to maintain the natural forest values as these values are neither assessed nor monitored, or control mechanisms specified (Gillman, 2008). In addition, no interest groups other than the Ministry for Primary Industries is involved in the approval process of sustainable forest management and there is no provision for appeal (Gillman, 2008).

The Forests Amendment Act 1993 further states that:

***"... the rate of harvest from a forest ... shall be limited to a level at which the forest can continue to supply an annual or periodic non-diminishing yield in perpetuity ..."*.**

This is interpreted in this thesis as: the overall basal area of the forest will recover after selective harvesting. There is evidence that this will indeed happen over time (M. C. Smale & Beveridge, 2007). However, a prerequisite even for 'yield' sustainability in uneven-aged forest is a continuous supply of trees across all diameter and age classes that are able to advance into higher classes. But the '*annual or periodic non-diminishing yield in perpetuity*' of the harvested species of podocarps is not achievable at Pureora, where a regeneration gap of podocarps is evident.

The next prescription in the Act states that:

"***harvesting shall, as far as possible, be restricted to the selective removal of trees predisposed to windthrow or early death***" while "***the character and structure of all parts of the forest shall be maintained***"

This seems to be a contradiction as senescent trees and in particular senescent emergent podocarps are an integral part of the podocarp-broadleaved forest at Pureora and habitat for numerous bird, invertebrate and plant species. As these trees are not currently being replaced by advancing podocarps, they are extremely valuable in the forest ecosystem. But the Forests Amendment Act softens this demand to '*as far as possible*', which transfers the decision to the forest manager. Those 'trees predisposed to windthrow and early death' arguably include the whole population of emergent podocarps at Pureora, as they reflect a senescent cohort of trees that are reaching the end of their natural life cycle.

In terms of regeneration in podocarp-broadleaved forest, the Act further states that if:

"***sufficient advanced growth is lacking, there shall be planted for each tree removed at least 5 nursery-raised seedlings of at least 60 centimetres in height of the same species***"

The findings of this doctoral study show that increasing light levels are a prerequisite for successful advanced growth of all podocarps, even if they are described as shade-tolerant in their early life stage. The gaps created by low-impact selective harvesting do not create habitats that favour podocarps. And in particular, where the light-demanding species *P. totara*, *D. dacrydioides* and *P. taxifolia* are harvested in small gaps, replanting of seedlings of those species is likely to be unsuccessful.

5.4. Requirements for successful podocarp regeneration

High-grading of the forest showed that *D. cupressinum* and *P. ferruginea* require gaps of 700-800 m² before they are able to outcompete *B. tawa*. For optimal growth they need gaps of 850-950 m² (15-21 % larger). The more light-demanding species *P. totara*, *D. dacrydioides* and *P. taxifolia* need even larger canopy gaps for successful establishment and subsequent growth. Gaps of these sizes are not compliant with the selective harvesting prescriptions of the Forests Amendment Act.

These gaps change the forest structure immensely and catastrophic disturbances such as the cyclone in 1936, high-grading or the cyclone Bola in 1988 prove that podocarps may need such large-scale disturbances for successful establishment and subsequent growth. Maintaining the current forest structure means inevitably maintaining the natural forest succession from a mixed podocarp-broadleaved forest to a broadleaved forest with only insignificant numbers of podocarps, unless another large-scale natural disturbance changes growth conditions in favour of the podocarps again.

This elaboration is neither a plea or even an excuse for future high-grading, nor for any other kind of large-scale harvesting operation. High-grading is unsustainable and where it has occurred has resulted in the collapse of the podocarp-broadleaved forest ecosystem (Figure 83). Large parts of the high-graded forest 56 years after harvesting are still covered by colonizing shrubs (*Coprosma* spp.) and pioneer tree species (*Carpodetus serratus*, *Cordyline australis*, *Pseudopanax arboreus*, *Schefflera digitata*, *Weinmannia racemosa*), tall grasses (*Austroderia fulvida*) and sedges (*Carex* spp.), without any indication that late successional species will appear in the foreseeable future.

Figure 83. Collapse of podocarp-broadleaved forest after high-grading with extensive soil compaction; this site was covered with old-growth forest until 1956; stumps and logs are still visible 56 years after high-grading

5.5. Conclusion and recommendation

The most important decision to be made when talking about the future of New Zealand's old-growth podocarp-broadleaved forest is the management question. Do we want to preserve the natural status of these forests or do we want to use the forest as an economic resource? Any silvicultural management system will inevitably change these complex ecosystems in one way or another. The NZ government already made the decision to cease all native forest harvesting operations on public land in 2002, and management is now restricted to the protection of native plant and wildlife. In native forests on privately owned land, the government permits harvesting as long as it is 'sustainable'. But the results of this doctoral research show that harvesting of senescent emergent podocarps in this forest type cannot be sustainable in any sense of the Forests Amendment Act. The scarcity of young and absence of medium age classes of podocarps, as evident in their regeneration gap, prohibits

harvesting of the emergent tier. Substantial numbers of dominant and co-dominant trees that ascend above the main canopy and into higher age and diameter classes are a prerequisite for sustainable forest management of uneven-aged forest. In particular, the light-demanding podocarp species are missing in all advanced life stages and occur only in their senescent phase. In addition, there are many bird, insect and plant species with different ecological requirements that depend on those trees as an irretrievable habitat and food source.

The results of this doctoral study demonstrate that it is time to review the current Forests Amendment Act in regard to sustainable harvesting of old-growth podocarp-broadleaved forests. The complexity of these forests has to be recognized and the ecological requirements of the different tree species involved. Also the specific natural successional trend of each forest, the scale of harvesting disturbance required and the definition of sustainability have to be discussed and incorporated. If old-growth podocarp-broadleaved forests are to be harvested, a clear definition of the desired target forest conditions is paramount and has to be used as a guideline for all silvicultural activities (Bauhus, 2014) and ethical frameworks have to be developed to assess management actions (Batavia & Nelson, 2016).

If indigenous forestry in uneven-aged podocarp-broadleaved forest aims to harvest podocarps at some stage in the future, the podocarp component of the forest has to be enhanced now while using a silvicultural approach that recognises the forest as a complex adaptive system (Messier, Puettmann, & Coates, 2013). Identifying the disturbance regime that is necessary for the successful recruitment of the different tree species (Martin & Ogden, 2006; Wells et al., 2001) is of utmost importance and should guide silviculture (Allen & Norton, 2000; R. J. Mitchell et al., 2002; Seymour, A. S. White, & deMaynadier, Philip, 2002; G. H. Stewart, 2002). The forest should be managed for old-growth attributes as they occur in close-to-nature concepts such as ‘Plenterwald’, ‘Dauerwald’ and ‘Continuous Cover Forestry’, which were developed and are practised successfully in Europe and North America (Bauhus, Puettmann, & Messier, 2009; Gadow, Nagel, & Saborowski, 2002; Reininger, 2000). A practical approach of such management would predominantly support site-specific natural

processes, assisted by active stand tending and regeneration regulation. The silvicultural toolbox is full of measures that are able to address those requirements (Barton, 2008; Bauhus et al., 2009; Messier et al., 2013; Puettmann, Coates, & Messier, 2009; Xabadia & Goetz, 2010), and some were already implemented in New Zealand by private land owners such as Rudolf Hohneck in *Agathis australis* forest in the Hunua Ranges as early as 1926 (Barton, 2007). Every silvicultural activity in the case of Pureora should focus on the successful recruitment of canopy species that currently show little ability to penetrate a dense canopy, in particular podocarps. Harvesting should be restricted to tree species that are abundant across all diameter classes (Beveridge & Herbert, 1978). At Pureora, the only species that fulfils this requirement is *B. tawa*. Harvesting and thinning will also have to go hand in hand across all diameter classes and desired individual trees should be released from competing neighbours where necessary.

A good example of possible management is given by The Tuhoe Tuawhenua Trust in Te Urewera in the eastern North Island (Carswell & Allen, 2010). The trust is managing podocarp-broadleaved forest that was high-graded in the 1950-60s (Rurehe, 2011). With a long-term goal that extends realistically to 200 years, it envisages the restoration of podocarps that are in severe decline in the forest (Lyver & Carswell, 2009; Tahi, 2011). Their management incorporates planting of seedlings as well as canopy manipulation through harvesting of *B. tawa* to support established podocarp saplings. Planting of seedlings should not be favoured over natural regeneration when a natural seed source is available, as nursery-raised seedlings are not adapted to the specific growth conditions at the planting site and are likely to undergo a phase of transplanting stress that can hamper their survival and slow their establishment. Soil characteristics such as soil phosphorus (P) and soil nitrogen (N) need to be recognized prior to planting as they can influence the growth of seedlings of the different species significantly (Carswell et al., 2007). Seedlings that established naturally and managed to survive and grow in the understorey for years are already winners of inter- and intraspecific competition and should be supported and preferred over planted individuals (H. D. Wilson, 2003).

In addition, the author of this doctoral research strongly recommends using the potential of native tree species for plantations. Early trials have proven to be very successful (Pardy, Bergin, & Kimberley, 1992) and recommendations for establishment of those trees are available (Bergin & Gea, 2007; Dodd & H. Ritchie, 2007). Under favourable conditions, the podocarp species show growth rates that exceed the observed rates in old-growth forest significantly (Bergin, 2003; Bergin & Kimberley, 2003), a potential that is also evident in the iconic gymnosperm *Agathis australis* (Bergin & Steward, 2004; Steward & Beveridge, 2010; Steward & Mckinley, 2005). Even if these growth rates will never be able to compete with those of extremely fast growing exotics such as *Pinus radiata* or the various eucalypts, the outstanding wood quality of several of New Zealand's native trees is far beyond that of any of the faster growing exotic species. The foresightful British forester David Ernest Hutchins emphasised the potential of native tree species in New Zealand for plantations as early as 1919 (Hutchins, 1919). Today, almost a hundred years later, his wise manifesto has not lost any of its actuality, and it is time to look ahead and make far-reaching decisions that will benefit not only the current generation of land owners and citizens but future generations of New Zealanders.

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Appendix

List of tree and tree fern species found at the study site

Scientific name	Common name
Gymnosperms (main canopy and subcanopy species)	
Dacrycarpus dacrydioides	kahikatea
Dacrydium cupressinum	rimu
Phyllocladus alpinus	Mountain toatoa
Phyllocladus toatoa	toatoa
Phyllocladus trichomanoides	tanekaha
Podocarpus totara	totara
Prumnopitys ferruginea	miro
Prumnopitys taxifolia	matai
Angiosperms (main canopy species)	
Beilschmiedia tawa	tawa
Elaeocarpus dentatus	hinau
Elaeocarpus hookerianus	pokaka
Knightia excelsa	rewarewa
Nestegis cunninghamii	Black maire
Nestegis lanceolata	White maire
Angiosperms (subcanopy, understorey and shrubs species)	
Alseuosmia pusilla	karapapa
Androstoma empetrifolia	Mountain mikimiki
Aristotelia serrata	Wineberry
Brachyglottis elaeagnifolia	
Brachyglottis kirkii var. kirkii	Kirks daisy
Brachyglottis repanda	rangiora
Carpodetus serratus	putaputaweta
Coprosma "oreophila"	
Coprosma dumosa	
Coprosma foetidissima	hupiro
Coprosma grandifolia	kanono
Coprosma lucida	shining karamu
Coprosma propinqua	
Coprosma rhamnoides	
Coprosma rigida	
Coprosma robusta	karamu
Coprosma rotundifolia	
Coprosma rugosa	
Coprosma tayloriae	
Coprosma tenuifolia	
Dracophyllum subulatum	Monoao

Scientific name	Common name
Fuchsia excorticate	Fuchisa
Gaultheria antipoda	Snowberry
Gaultheria depressa var. "novae-zelandiae"	Mountain snowberry
Gaultheria macrostigma	
Griselinia littoralis	Broadleaf
Griselinia lucida	
Hebe corriganii	Purple-flowered hebe
Hebe stricta var. stricta	koromiko
Hedycarya arborea	Pigeonwood
Kunzea ericoides s.l.	kanuka
Leptecophylla juniperina ssp. juniperina	Prickly mingimingi
Leptospermum scoparium	manuka
Leucopogon fasciculatus	mingimingi
Melicope simplex	poataniwha
Melicytus lanceolatus	mahoe-wao
Melicytus ramiflorus	mahoe
Myrsine australis	Red mapou
Myrsine divaricata	Weeping matipo
Myrsine salicina	toro
Neomyrtus pedunculata	rohutu
Olearia arborescens	Glossy tree daisy
Olearia ilicifolia	Mountain holly
Olearia rani var. colorata	heketara
Ozothamnus vauvilliersii	Mountain cottonwood
Pennantia corymbosa	kaikomako
Pentachondra pumila	
Pittosporum eugenioides	Lemonwood
Pittosporum kirkii	Thick-leaved kohuhu
Pittosporum tenuifolium	
Pseudopanax arboreus	Five-Finger
Pseudopanax colensoi	Mountain three finger
Pseudopanax crassifolius	Lancewood
Pseudopanax edgerleyi	
Pseudowintera axillaris	horopito
Pseudowintera colorata	Pepperwood
Quintinia serrata	Westland quintinia
Raukaua anomalus	whauwhaupaku
Raukaua simplex	haumakoroa
Schefflera digitata	Sevenfinger
Weinmannia racemosa	kamahi
Monocotyledonous tree species	
Cordyline australis	Cabbage tree
Cordyline indivisa	Broad-leaved cabbage tree

Scientific name	Common name
Tree ferns	
Cyathea dealbata	Silver fern
Cyathea smithii	Soft-leaved tree fern
Dicksonia fibrosa	wheki-ponga
Dicksonia squarrosa	wheki